

# The lizard microbiome: patterns, drivers, and functional implications

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Editor: Clare Taylor

## Abstract

The lizard microbiome is a dynamic community that plays a crucial role in the health and survival of these animals. As global change poses significant threats to lizard populations around the world, understanding the interactions between lizards and their microbial communities is increasingly important. Here, we synthesize a rapidly growing body of research on the composition, diversity, transmission, and functional roles of lizard microbiomes. We discuss the implications of microbiome variation for lizard physiology, as well as the potential for microbiomes to inform conservation strategies for threatened species. Finally, we highlight priorities for future research, which include the need to quantify microbiome diversity and function across additional taxa, as lizards remain under-represented in the microbiome literature. We also stress the importance of experimental and field research that can reveal the adaptive significance of lizard microbiomes in the face of environmental change. Our synthesis highlights the contributions of lizard microbiome science to the fields of ecology, evolution, and conservation biology and demonstrates how the microbial communities that live in and on lizards enhance our understanding of their biodiversity and inform efforts to protect vulnerable populations.

**Keywords** host-associated microbiota, host-microbe interactions, microbial diversity, symbiosis, squamate

## Introduction

The study of microbiomes has gained significant traction in recent years, revealing intricate relationships between host organisms and the microbes that live in and on their bodies. Host-associated microbiomes are shaped by a variety of host and environmental factors and influence physiology, behavior, and fitness, making them central to understanding ecology and evolution across the tree of life (Ley et al. 2008, Fontaine and Kohl 2020, Song et al. 2020, Bornbusch et al. 2023). Lizards represent one of the most speciose groups, with over 7000 described species distributed across every continent except Antarctica, and occupying environments from arid deserts to tropical forests, coastal dunes, and urban centers (See Poe et al. 2017, Guedes et al. 2024, Uetz et al. 2025 for further detail on lizard diversity). They exhibit remarkable variation in body size, thermal physiology, diet, reproductive mode, and life history strategy. This combination of taxonomic breadth, wide geographic distribution, and ecological diversity makes lizards an ideal group for investigating how host evolution, ecology, and environment jointly shape gut microbiome structure and function.

A growing body of literature has begun to reveal patterns in the composition and diversity of lizard microbiomes, as well as their potential influence on host health and physiology (Ren et al. 2016,

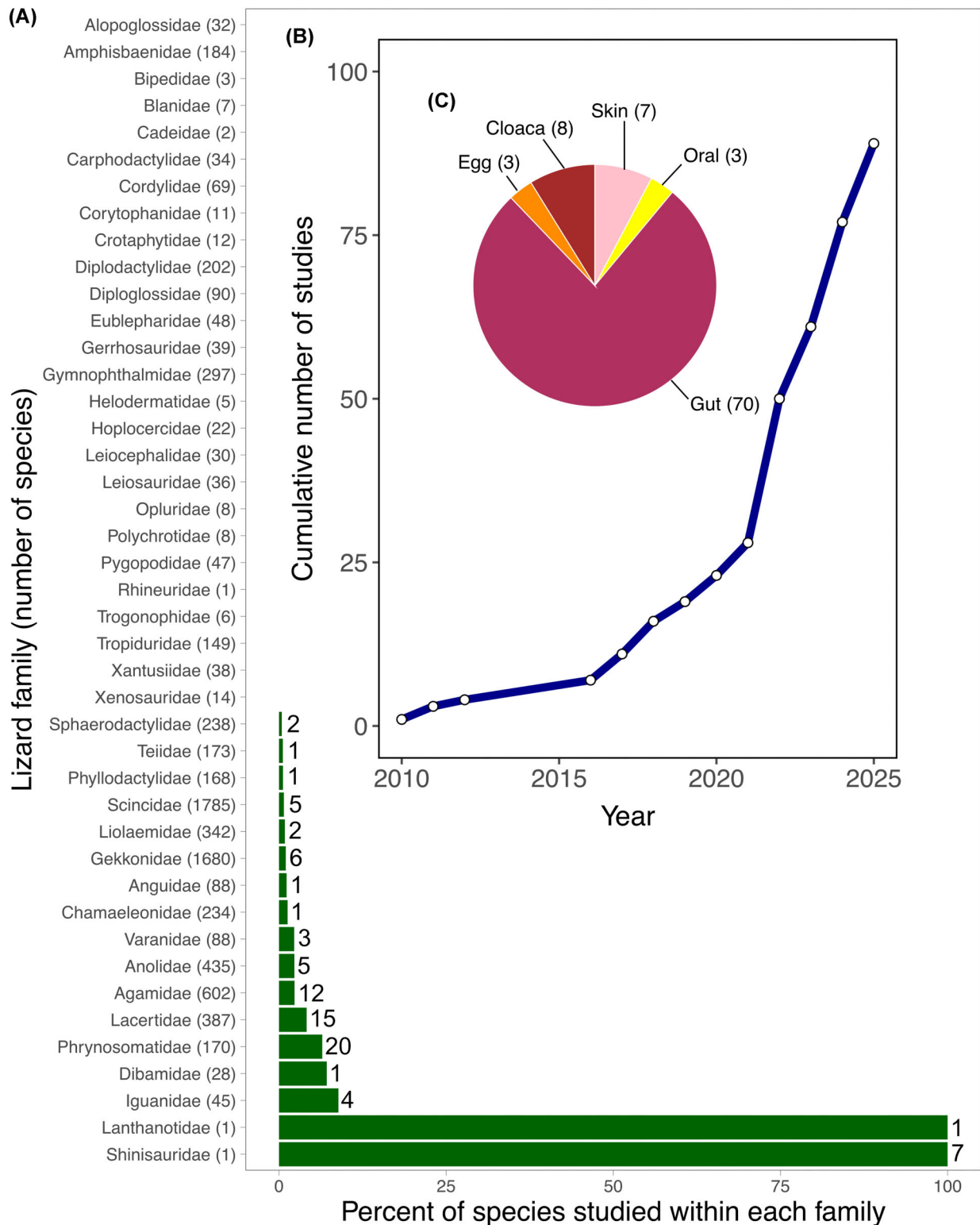
Kohl et al. 2017, Moeller et al. 2020, Bunker et al. 2022, Chen et al. 2022, Williams et al. 2022, Vasconcelos et al. 2023). Most studies are species-specific and we therefore lack an integrated understanding of lizard-microbiome interactions across host taxa. Here, we synthesize current research on lizard microbiomes, with a special focus on gut microbiomes given their importance to hosts and the fact that most studies have sampled the gut. Further, we focus on the bacterial component of the microbiome given that very few studies have assessed the presence and prevalence of other types of micro-organisms (Table S1). We review the environmental and host factors shaping these communities and their potential functional roles in lizard physiology and fitness. We aim to highlight knowledge gaps and propose priorities for future work that will enhance our understanding of lizard-microbiome interactions.

## The state of microbiome research across lizard taxonomic and geographic diversity

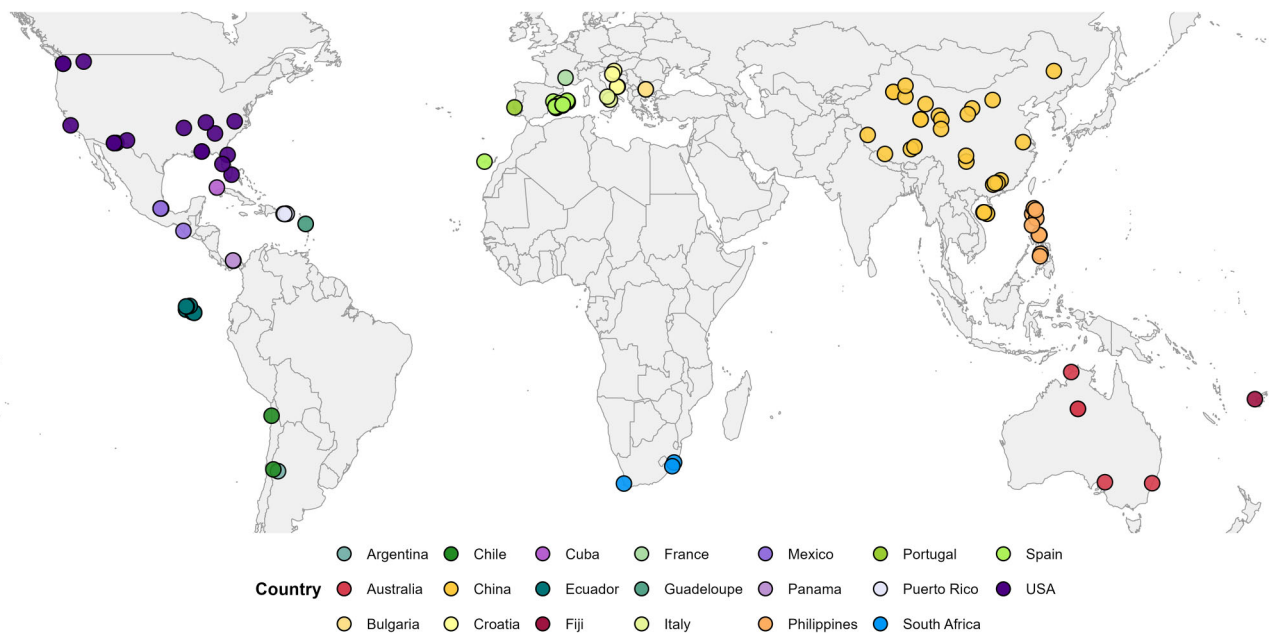
The body of literature on lizard microbiomes has grown substantially in recent years (Fig. 1B). We identified 89 studies which examined the microbiome of at least one lizard species (see Table S1

Received: 7 November 2025. Revised: 2 February 2026. Accepted: 12 March 2026

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**Figure 1** The number of lizard microbiome studies research has grown substantially in recent years, but lizard taxa and body sites are not evenly represented. Lizard microbiome studies are restricted to 17 out of 43 lizard families (based on Uetz et al. 2025). Even within families which have been surveyed, studies have covered only a small percentage of the species diversity within each family. (A) Percent of species within lizard families with at least one microbiome study (numbers indicate total number of studies on at least one species within each family). (B) Plot of cumulative lizard microbiome studies over time. (C) Proportion of studies surveying different lizard body sites.



**Figure 2** Lizard microbiome studies are predominantly restricted to the Northern Hemisphere. Each point represents a wild collection location at which one or more lizard species were sampled; in some cases, individual studies contributed multiple sampling sites. Number of sites by region: North America = 23, Central America = 5, South America = 6, Europe = 15, Africa = 4, East Asia = 23, Southeast Asia = 2, and Oceania = 6.

for a comprehensive list of studies and literature search methodology). Despite this growth, research on lizard microbiomes is disproportionately sparse compared to that of other vertebrate classes, such as mammals (~1111 gut microbiome studies, ~5000 species), birds (~830 gut microbiome studies, ~10 000 species) (Colston and Jackson 2016, Degregori et al. 2025), and even amphibians (~3581 studies across all body sites, with ~8000 species; Woodhams et al. 2020). Consequently, the vast majority of lizard diversity remains severely understudied. Studies have surveyed species within 17 of the 43 families in the suborder Sauria (Fig. 1A), accounting for only 103 of the 7859 lizard species—just 1% of total lizard diversity (Uetz et al. 2025).

Geographic coverage is similarly uneven (Fig. 2). Even though lizards are found almost everywhere on earth, most studies have been conducted in the Northern Hemisphere, particularly North America, parts of Asia, and Europe. There has been only scattered samplings of Southern Hemisphere species and entire regions remain unsampled, including areas of extremely high biodiversity like neotropical rainforests. This geographic bias limits the generalizability of findings and addressing these taxonomic and geographic gaps is crucial for developing a comprehensive understanding of lizard microbiomes.

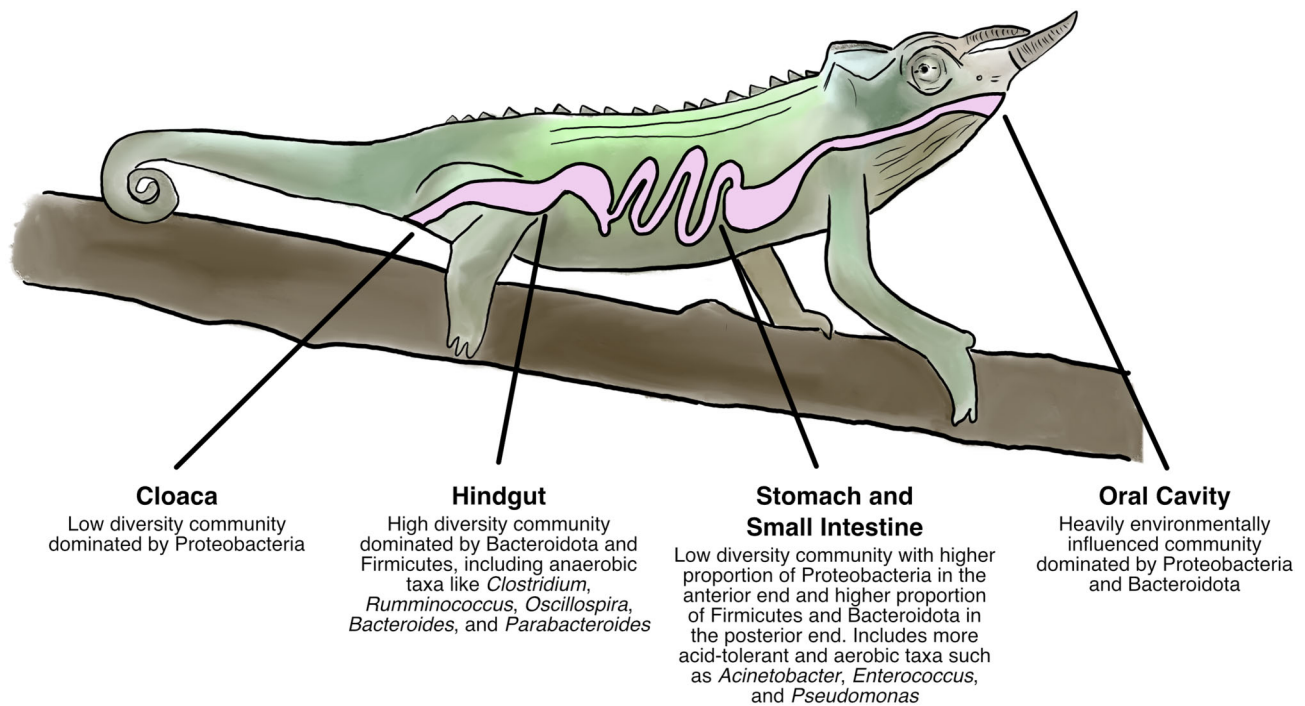
## General trends in lizard microbiome composition and diversity across body sites

Despite microbial variation across body sites (Colston and Jackson 2016), most lizard microbiome studies focus on the gut (Fig. 1C, Table S1). A recent meta-analysis of gut microbiome surveys across all reptiles found that their microbiomes are dominated by three key microbial phyla: Bacteroidetes, Proteobacteria,

and Firmicutes, consistent with studies of other vertebrates (Hoffbeck et al. 2023). The phyla Bacteroidetes and Firmicutes are common gut residents that include taxa capable of degrading complex carbohydrates (Hernández et al. 2023). Within Squamata specifically, more than 70% of individuals studied hosted the genus *Bacteroides*, suggesting an important role for this genus (Hoffbeck et al. 2023, 2025).

The gastrointestinal tract varies in function, morphology, and chemical environment across its length (O'Grady et al. 2005, Wehrle et al. 2020). In turn, microbial community diversity and dominant taxa shift across the transitions between functional zones of the gut (Fig. 3). The stomach and small intestine host less diverse microbial communities with higher prevalence of Proteobacteria and may include acid-tolerant, aerotolerant, or facultatively anaerobic genera like *Acinetobacter*, *Enterococcus*, and *Pseudomonas* (Kohl et al. 2017, Hernández et al. 2023). The hindgut hosts the most diverse microbial community (Kohl et al. 2017, Hernández et al. 2023) and is typically dominated by the phyla Bacteroidetes and Firmicutes (Kohl et al. 2017, Zhang et al. 2021). The cloaca might host a distinct microbiome, and limited data suggest that cloacal microbial communities are less diverse and dominated by Proteobacteria and Enterobacteriaceae (Bunker et al. 2022; Lazarkevich et al. 2024a, 2024b).

Given the variation in the gut microbiome along the digestive tract, the sampling strategy used in a particular study is important. Sampling strategies are diverse, including whole gut samples from dissections, fecal samples, cloacal swabs, and cloacal flushes. Fecal samples can be a good proxy of the gut microbiome in some species but may overrepresent hindgut taxa (Kohl et al. 2017, Zhang et al. 2021; Hernández et al. 2023, 2025). Cloacal swabs may also serve as sufficient proxies of the gut microbiome, but whether or not the animal has recently defecated can affect results (Bunker et al. 2022, Hernández et al.



**Figure 3** Microbial biogeography of the lizard gastrointestinal tract. Artwork by CE Williams, depicting a Jackson's chameleon (*Trioceros jacksonii*).

2023). Altogether, if an understanding of fine scale variation is needed to explore functional relationships between gut taxa and hosts, dissection of gut regions may be a useful approach (although non-destructive sampling may be required for threatened species).

Few studies have assessed microbial composition of body sites other than the gut. These studies, limited to only 14 species from multiple families, including Chamaeleonidae, Iguanidae, Agamidae, Shinisauridae, Scincidae, and Gekkonidae (Table S1), reported that the skin and oral cavities had high proportions of Proteobacteria, although composition was variable and heavily influenced by the environment (Hyde et al. 2016, Weitzman et al. 2018, Jiang et al. 2022, Tian et al. 2022, Weitzman et al. 2025a, 2025b). In the Chinese crocodile lizard (*Shinisaurus crocodilurus*), captivity-induced loss of diversity and reduced prevalence of Actinobacteria and Acidobacteria in the skin microbiome was associated with skin ulcers (Jiang et al. 2022, 2025). These ulcers are caused by *Pseudomonas aeruginosa*, and the prevalence of this condition was reduced by use of probiotics, suggesting that skin microbiota play a role in preventing proliferation of pathogenic taxa (Xiong et al. 2022). Overall, microbiomes aside from the gut remain poorly studied, and further research is needed to assess their stability, ecological importance, and functional roles.

## Mechanisms of transmission of lizard microbiota

Like other vertebrates, lizards acquire microbes during development through both vertical (i.e. from parents) and horizontal (i.e. from other individuals and the environment) transmission modes. Understanding patterns of microbiome heritability has implications for host evolution (Morris and Bohannan 2024) and early-life

microbial exposures can have long-term consequences for host physiology and fitness (Fontaine and Trevelline 2025).

## Vertical transmission

Vertical microbiome transmission occurs when microbes are passed from parent to offspring. In a study of viviparous lizards (*Liolaemus parvus*, *L. ruibali*, *Phymaturus williamsi*), 34% of the microbial taxa found in offspring feces were also found in their mother's feces (Kohl et al. 2017). In the oviparous striped plateau lizard (*Sceloporus virgatus*), maternal identity explained 21% of the variation in hatchling microbiota, with 35% of amplicon sequence variants (ASVs) sourced from the maternal cloaca (Bunker and Weiss 2024). Some ASVs may also be transmitted via egg contents (Trevelline et al. 2018) or during embryonic development (Montoya-Ciriaco et al. 2023). However, the ability of live microorganisms to be transmitted to embryos during development remains an area of active debate in the field of microbiome science (Perez-Muñoz et al. 2017, Blaser et al. 2021). Although microbiome heritability has not been directly tested in lizards, the presence of vertical transmission in this group presents the possibility for faithful passage of microbiota from one generation to the next. If microbes are heritable and influence host fitness, these communities may influence the evolution of their hosts (Morris and Bohannan 2024).

## Horizontal transmission

The lizard microbiome can be further shaped by horizontal transmission from conspecifics, heterospecifics, or environmental sources. Heterospecific coprophagy has been observed in several lizard species, including Cuban green anoles (*Anolis porcatius*) (Armas 2021), Australian Water Dragons (*Intellagama lesueurii*) (Baxter-Gilbert 2014) and members of the genus *Gallotia* (Mamin

and Rodriguez 2021). Conspecific cannibalism, seen in species like Lilford's and Skyros wall lizards (*Podarcis lilfordi*, *P. gaigeae*) (Cooper et al. 2015) and *Gallotia caesaris* (Mateo and Pleguezuelos 2015), may also facilitate microbiome transfer within species. Lizards can also acquire microbes from environmental sources, such as plants and invertebrate prey (Kohl et al. 2017).

## Host drivers of microbiome composition and diversity

### Phylogeny

Host species identity and evolutionary history are major determinants of gut microbiome composition in most animals (Ley et al. 2008). Species-specific traits create unique microbial niches, leading to distinct microbiomes even among closely related species. This pattern underlies the concept of phylosymbiosis, where the similarity of microbial communities reflects the evolutionary relationships of their hosts (Lim and Bordenstein 2020). In lizards, studies comparing different host species often find that they each have distinct gut microbiome compositions (Hong et al. 2011, Lankau et al. 2012, Ren et al. 2016, Kohl et al. 2017, Baldo et al. 2018, Bunker and Weiss 2022, Eliades et al. 2022; Hernández et al. 2022, 2024, Lazarkevich et al. 2024c, Vasco et al. 2022, Härer et al. 2023, Vasconcelos et al. 2023). However, environmental factors can sometimes override phylogenetic effects on gut microbiomes (Qi et al. 2020). Bunker and Weiss (2022) found that conspecifics in close sympatry shared 41.0% of their ASVs, different species in sympatry shared 21.5% of their ASVs, and conspecifics in allopatry shared only 10%–12% of their ASVs. This high degree of environmental-influence may be the reason that phylosymbiosis patterns in lizards are often weak (Ren et al. 2016) or undetected (Eliades et al. 2022, Hoffbeck et al. 2023, Smith et al. 2025).

### Sex

While evolutionary history structures gut microbiomes broadly across the tree of life, sex can further modulate microbial communities within individual species. Some species of lizard exhibit strong sex-based differences in morphology, ecology, and physiology (Scharf and Meiri 2013, Logan et al. 2021). While it follows that sex might also affect the structure and diversity of the gut microbiome in lizards, surprisingly, this does not seem to be the case in most species (Table S2). In a few species, including the striped plateau lizard (*Sceloporus virgatus*) females had unique microbial community compositions characterized by lower diversity and richness (Zhang et al. 2022a, Martin et al. 2010). However, a follow up study on striped plateau lizards using more robust sequencing methods found the opposite pattern: higher diversity and richness in females, suggesting that these patterns might be sensitive to methodology (Bunker et al. 2022). Importantly, the effect of sex was not tested in a relatively large number of studies where lizards of both sexes were collected.

### Body size

Body size is known to affect microbiome composition in animals, with larger body size associated with greater microbiome diversity

(Reese and Dunn 2018, Sherrill-Mix et al. 2018). Larger hosts have larger guts, longer transit times, and greater niche space for colonization by diverse microbial taxa (MacArthur and Wilson 1967, Sherrill-Mix et al. 2018). In lizards, studies have investigated body size effects at both intra- and interspecific scales, with mixed results. At the intraspecific level, among five species of Portuguese lacertids, only one (*Podarcis siculus*) showed a significant relationship between body size and microbiome diversity, with larger individuals having higher Shannon diversity (Vasconcelos et al. 2023). Similarly, body size was correlated with microbiome composition but not diversity in the striped plateau lizard (Bunker et al. 2022). Because lizards experience indeterminate growth, body size can be strongly correlated with age, which may make disentangling the effects of body size and age difficult. At the interspecific level, in gekkonids, smaller-bodied species hosted more diverse microbiomes (Eliades et al. 2022). However, when comparing across species, patterns may be confounded by factors such as diet, gut transit time, and species-specific allometric differences in gut length relative to body size. Altogether, body size does appear to play a role in shaping the microbiome of lizards. However, its effects are context-dependent and potentially driven by correlated variables.

### Ontogeny

As animals age, they are often faced with differing environmental challenges and physiological needs, and their gut microbiomes can shift in response (Dasari et al. 2025). Nonetheless, studies on lizards have not consistently found shifts in microbiomes over ontogeny. For example, Tang et al. (2020) found no differences in gut microbiome composition between juvenile and adult Chinese crocodile lizards. In contrast, Baldo et al. (2023) reported that life stage significantly influenced microbiome composition in Balearic wall lizards (*Podarcis lilfordi*). It is possible that differences in microbiome responses to ontogeny are affected by how much ecological variation individuals experience across the lifespan. However, in eastern fence lizards (*Sceloporus undulatus*), Assis et al. (2023) found that older individuals had lower diversity microbiomes compared to younger individuals, despite being raised in a homogeneous environment. Together, these studies suggest that while age can influence microbiome structure in lizards, its effects may vary among species and depend on environmental context.

### Mating strategy

Recent studies on lizard microbiomes reveal intriguing connections between mating behavior and microbial communities. In the striped plateau lizard, reproductive season affected microbiome composition, with lower diversity during mating periods (Bunker et al. 2022). In the common lizard (*Zootoca vivipara*), polyandrous females harbored more diverse and variable cloacal bacteria than monandrous females, likely due to sexual transmission from multiple mates (White et al. 2011). Together, these studies highlight that mating behavior can significantly shape microbiome structure, though the effects vary by species.

## Environmental factors shaping lizard gut microbiomes

### Elevation

The effect of elevation on gut microbiome composition in lizards has been tested in several studies, predominantly in toad-headed lizards (genus *Phrynocephalus*) from Central and East Asia. Across these systems, gut microbial community composition was consistently structured by elevation, although alpha diversity was not. Several studies found that higher elevation Qinghai toad-headed lizards had lower microbial diversity (Zhang et al. 2018a, Yu et al. 2025). In contrast, (Montoya-Ciriaco et al. 2020) found no variation in alpha diversity across an elevational gradient in mesquite lizards (*Sceloporus grammicus*) from central Mexico, although some taxa varied in abundance. In all of the aforementioned studies, as well as two additional studies on toad-headed lizards (Qi et al. 2020, Du et al. 2025), microbial community composition differed between sites at different elevations. Du et al. 2025 also linked these microbial shifts to differences in host metabolic function, with high-elevation Yarkand toad-headed agamas (*Phrynocephalus axillaris*) exhibiting unique metabolomic profiles related to amino acid and lipid metabolism. Collectively, these studies suggest that elevation can strongly influence the gut microbiomes of lizards. It is possible these changes are adaptive because the microbiome can influence energy metabolism and thermal tolerance (Zhang et al. 2018b, Li and King 2025) which may be important in high elevation environments, but this idea remains to be tested.

### Urbanization and Anthropogenic Stressors

Urbanization and other human-driven environmental changes have been increasingly studied as a driver of microbiome structure across animal species, including lizards. A study of crested anoles (*Anolis cristatellus*) found that urban populations exhibited gut microbiomes more similar to those of humans than rural lizards (Dillard et al. 2022). Vasconcelos et al. 2023 found that three species (*Podarcis siculus*, *P. virescens*, and *Teira dugesii*) of lizards living in an urban environment harbored significantly higher bacterial diversity compared to two related species living in a rural environment. However, responses are not uniform: some dwarf chameleons like *Bradypodion melanocephalum* show strong habitat-related associations while others such as *B. setaroi* do not, underscoring species-specific sensitivity to urban environments (Adair et al. 2025). The effects of urbanization may be in part driven by environmental pollutants. In the green anole (*Anolis carolinensis*), TNT exposure reduced microbial diversity and enriched detoxifying taxa (Indest et al. 2018). Pyrethroid pesticides in the Mongolia racerunner (*Eremias argus*) altered gut composition, metabolites, and neural gene expression (Chang et al. 2025). Together, these findings suggest that while urbanization and pollutants can substantially remodel lizard microbiomes, the magnitude and consequences vary across species and stressors.

### Seasonality

Seasonal shifts can alter climatic regimes and dietary options leading to changes in gut microbiota composition. Moreover, lizard

physiology can change across seasons and drive further changes in microbiomes. Because physiological responses to seasonality can be idiosyncratic across the tree of life, concomitant changes in microbiomes are generally species-specific. In a study of four *Sceloporus* species, transitions between the dry and rainy season produced species-specific responses in both alpha and beta diversity (Hernández et al. 2024). In Balearic wall lizards (*Podarcis pityuensis*), multiple populations were tested and showed seasonal shifts in microbial composition, mainly in the relative abundances of fermentative bacteria (Baldo et al. 2023). In the Reeve's butterfly lizard (*Leiolepis reevesii*), microbial composition shifted markedly during winter hibernation, including increased abundance of Verrucomicrobia and Bacteroidetes and decreased abundance of Firmicutes (Zhu et al. 2024b). Dietary shifts to frugivory in autumn prior to hibernation were linked to compositional changes and altered metabolite profiles in the Turpan wonder gecko (*Teratoscincus roborowski*; Gao et al. 2023). Conversely, in the striped plateau lizard, hibernation had no effect on gut microbiome composition, which was instead predominantly affected by the reproductive season (Bunker et al. 2022). Finally, in sleepy lizards (*Tiliqua rugosa*), the richness and prevalence of Enterobacteriaceae in the cloaca increased progressively across the active season (Lee et al. 2024). Overall, seasonality interacts with diet and physiology to shape lizard microbiomes, but its effects differ among species and populations.

### Temperature

Environmental temperature is widely documented to affect gut microbiomes (Sepulveda and Moeller 2020). This may be disproportionately true for ectotherms like lizards, whose body temperatures vary with environmental temperature. However, how environmental temperature influences lizard gut microbiomes varies. Some studies identified decreased richness under warming (Zhang et al. 2022b, Bestion et al. 2017, Fromm et al. 2024) while others detected an increase (Zhu et al. 2024a, Lin et al. 2023), and still others found no impact of warming (Zhu et al. 2024a, Moeller et al. 2020, Chen et al. 2022, Liu et al. 2022, Williams et al. 2022). Similarly, responses of community composition to warming range from strong (Zhang et al. 2022b, Zhu et al. 2024a, Moeller et al. 2020, Liu et al. 2022), to weak (Bestion et al. 2017, Lin et al. 2023, Fromm et al. 2024, Yang et al. 2024) to negligible (Chen et al. 2022, Williams et al. 2022). Differences in study design might explain the variation in observed temperature effects. For example, microbiome profiles generated from fecal samples responded differently to warming than those from intestinal samples (Zhu et al. 2024a, 2024b). Experimental temperature (Lin et al. 2023), exposure length (Yang et al. 2024), and access to thermal refugia (Fromm et al. 2024) can also shape experimental results. In general, research has demonstrated that while acute heat stress can destabilize microbial communities, the ecological context determines whether microbiomes confer resilience or vulnerability to increasing temperatures.

### Precipitation

Although no experiment has yet been conducted demonstrating that precipitation affects lizard microbiome variation on its own, a study on Panamanian slender anoles (*Anolis apletophallus*) revealed that a severe drought correlated with significant changes

in lizard gut microbial community composition (Williams et al. 2022). These results suggest that precipitation can shape host-associated microbiomes, although whether the effects are direct or indirect (i.e. mediated by changes in diet) remains to be tested.

## Diet

Lizards exhibit remarkable dietary variation that can strongly influence their gut microbiota. Lizard species can be herbivorous, omnivorous, or carnivorous. Most lizard species are carnivorous and consume small arthropods although several groups consume vertebrate prey (e.g. Varanids, Crotaphytids). Based on the limited number of species studied to date, plant-rich or broader diets appear to be associated with higher microbial diversity and enrichment of fiber-degrading taxa, although this pattern has not yet been tested across a wide taxonomic or ecological range. Omnivorous Italian wall lizard (*Podarcis siculus*) populations exhibit greater gut diversity than insectivorous populations (Lemieux-Labonté et al. 2022) and Galápagos land iguanas (*Conolophus subcristatus*) host more diverse, fiber-degrading bacteria compared to algae-consuming marine iguanas (*Amblyrhynchus cristatus*; Hong et al. 2011, Lankau et al. 2012, Vasco et al. 2022). Similarly, the omnivorous Columbrete wall lizard (*Podarcis liolepis*) harbors gut bacteria linked to plant polymer degradation (Bassitta et al. 2022).

Within lizard species, seasonal diet changes drive parallel microbiome changes (Gao et al. 2023, Wang et al. 2024). In the Mesquite lizard and Trans-volcanic bunchgrass lizard (*Sceloporus bicanthalis*), increased dietary richness during the rainy season correlated with greater bacterial richness (Hernández et al. 2024). In the Reeves's butterfly lizard, winter fasting coincided with an increase in mucin-degrading bacteria, while summer omnivory led to enrichment of fiber-degrading Firmicutes (Zhu et al. 2024b). Controlled feeding trials have also been used to causatively link shifts in diet to shifts in microbiome composition. In the Borneo earless monitor lizard (*Lanthanotus borneensis*), fish and shrimp diets increased bacterial diversity and relative abundance of the phyla Firmicutes, while an earthworm diet led to Proteobacteria dominance (Diana et al. 2025). Experimental feeding trials in water monitor lizards (*Varanus salvator*; Du et al. 2021), Japanese geckos (*Gekko japonicus*; Jiang et al. 2023), *Liolaemus* and *Phymaturus* species (Kohl et al. 2017), *Podarcis* lizards (Buglione, Ricca and Petrelli 2022), and crocodile lizards (Jiang, Ma and Li 2017) further support diet-dependent microbial community shifts.

In some cases, diet shifts alter physiology and morphology through microbiota changes, as gut bacteria modify metabolic processes that influence host traits (Holmes et al. 2019). For example, juvenile Chinese crocodile lizards fed a centipede-enriched diet grew faster and had better body condition than those on an earthworm-only diet, likely due to enrichment of fermentative gut bacteria. These bacteria can break down complex dietary components into short-chain fatty acids that can be directly metabolized by the host (Xie et al. 2024). In Ruibal's tree iguana (*Liolaemus ruibali*), a plant-rich diet promoted fiber-degrading bacteria, likely facilitating herbivory-related traits such as intestinal elongation (Kohl et al. 2016). Overall, studies in this area suggest a diet-microbiome-host function axis, but this framework remains based on a narrow set of taxa.

## Captivity

Studies have demonstrated that captivity alters community composition of lizard gut microbiomes (Ren et al. 2016, Kohl et al. 2017, Tang et al. 2020, 2022, Zhang et al. 2022a, Eliades et al. 2021) and can lead to changes in dominant phyla including reduced abundance of Firmicutes and increased abundance of Bacteroidetes (Zhang et al. 2022a, Kohl et al. 2016, Tang et al. 2020). Captivity also results in decreased inter-individual variation in microbiomes (Ren et al. 2016, Eliades et al. 2021). The amount of time individuals spend in captivity might affect the amount of change in their gut microbiomes. Microbiomes may remain stable over short periods of captivity (Williams et al. 2022) but diverge substantially after longer timescales (>2 months; Zhang et al. 2022b). Compared to findings on microbial community composition, the effects of captivity on alpha diversity are less consistent, with studies finding increases (Tang et al. 2020, 2022; Du et al. 2021), decreases (Ren et al. 2016), or no difference based on captivity status (Zhang et al. 2022a, Kohl et al. 2017). Interestingly, gut microbial communities can revert to wild-like states following reintroduction (Eliades et al. 2021, Forehand et al. 2025). Understanding captivity-induced changes in gut microbiomes is important, as these changes can have implications for the health of animals in human care and the success of conservation breeding programs (Bahrndorff et al. 2016).

## Implications of lizard microbiomes for host biology

### Gestation

The lizard gut microbiome can change significantly during gestation. In eastern fence lizards, gravid females exhibited reduced microbial diversity and increased variability in gestation, potentially reflecting trade-offs between reproduction and microbiome stability (Trevelline et al. 2019). Glucocorticoid (CORT) exposure further alters the microbiome, with effects varying by reproductive state, reducing diversity in general but increasing it in late-gestation lizards (MacLeod et al. 2022). Specific microbes shift under CORT exposure in gravid females, highlighting the microbiome's potential role in mediating stress during gestation. Collectively, these findings suggest that microbiomes change during gestation, with implications for maternal and offspring health.

### Thermal tolerance

Links between the gut microbiome and lizard thermal tolerance have been studied in several lizard species. In western fence lizards (*Sceloporus occidentalis*) microbiome composition was correlated with heat tolerance (critical thermal maximum;  $CT_{max}$ ; Moeller et al. 2020). However, in the Panamanian slender anole, there was no relationship between thermal tolerance (voluntary thermal maximum) or thermoregulatory behavior and either gut microbiome composition or diversity (Williams et al. 2022). Despite not identifying a direct physiological link, Bestion et al. 2017 showed that losses of bacterial diversity at high temperatures were correlated with reduced lizard survival.

## Metabolic rate

Gut microbes may influence lizard metabolic rate and energy balance, although the studies testing these links have produced limited and conflicting results. Liu et al. (2022) found that warming affected physiology and microbiome structure in two species of lizards: open habitat Mongolian racerunners showed higher metabolic rates with minimal microbiome change, while semi-closed habitat Amur grass lizards (*Takydromus amurensis*) had lower metabolic rates and altered microbial functional potential, suggesting a possible compensatory role of the microbiome. However, this evidence was correlational and based on microbial functions inferred from 16S data, which can be imprecise. The only other study to investigate the relationship between microbiome composition and metabolism was in Qinghai-Xizang Plateau lizards (*Phrynocephalus vlangalii*), where resting metabolic rates did not differ across elevation, despite differences in microbiomes (Yu et al. 2025).

## Immunity and disease

A key role of the microbiome is priming and training the immune system to respond to pathogens (Belkaid and Hand 2014), and this process also appears to be important in at least one species of lizard. In multi-ocellated racerunners (*Eremias multiocellata*), fecal transplants revealed that shifts in gut microbiota composition were linked to enhanced antibacterial activity and increased expression of immune-related genes, suggesting that gut bacteria can modulate systemic immunity (Yang et al. 2024). Microbes may also contribute to pathogen colonization resistance, including at the egg stage. In the striped plateau lizard, transmission of bacteria from mother to offspring via egg surfaces reduced fungal colonization, in turn resulting in greater hatching success and larger offspring (Bunker et al. 2021, Bunker et al. 2022, Boulet et al. 2025). Microbes isolated from lizards have shown broad-spectrum antimicrobial properties (Akbar et al. 2019). However, the microbiome can also harbor latent pathogens that the immune system must constantly suppress. For example, a strain of *Pseudomonas aeruginosa* isolated from a healthy common wall lizard (*Podarcis muralis*) possessed potent virulence factors, highlighting its potential to cause disease if host immunity is compromised (Lazarkevich et al. 2024c). These studies suggest that microbiomes may play a key role in the immune responses of lizards and that their immune systems must balance the control of opportunistic pathogens with the potential for harnessing beneficial microbes.

## Growth rate

The gut microbiome might influence lizard growth rates. In Qinghai-Xizang Plateau lizards, offspring moved to lower elevations grew faster than those moved to higher elevations, likely aided by the bacterial genus *Citrobacter*, which may enhance energy storage and nutrient availability (Yu et al. 2025). Moderate warming boosted growth in Mongolian racerunners and Amur grass lizards, and was associated with a restructuring of the gut microbiome, characterized by a reduction in pathogenic Enterobacteriales order and an enrichment of probiotic taxa potentially supporting higher metabolic demands and nutrient absorption (Liu et al. 2022). In juvenile Chinese crocodile lizards, a centipede-based

diet led to an increase in fermentative bacteria and faster growth without increased food consumption, suggesting a direct microbial role in enhancing energy absorption and growth (Xie et al. 2024). Together, these studies suggest that the lizard gut microbiome plays a role in optimizing host energetics, stress resilience, and nutrient absorption.

## Gaps and priorities

It is evident that host traits and environmental factors both shape lizard gut microbiomes, and these communities can in turn influence host phenotypes. However, many gaps remain in our understanding of lizard gut microbial ecology. While most research has focused on the gut, likely due to its direct links to host physiology, a significant gap exists in our knowledge of microbiomes from other body sites (e.g. skin, oral cavity, respiratory and reproductive organs). This knowledge gap is problematic as microbiomes have been implicated in skin and respiratory diseases of other reptiles (i.e. snakes, tortoises; Siddiqui et al. 2022, Romer et al. 2025), and the extent to which microbes in non-gut body regions influence disease ecology, microbial transmission, and adaptation to environmental change in wild lizard populations is virtually unknown.

Although research on host-associated microbiomes has expanded rapidly, comparatively little attention has been given to identifying generalizable patterns across host lineages. Instead, much of the existing literature highlights species-specific patterns, underscoring the highly contingent nature of host-microbiome interactions and revealing a major gap in our understanding of whether broader organizing principles exist. The influence of host sex is still unclear, as many studies did not explicitly test for sex effects, and those that did reported conflicting results. This is a particularly promising area of potential research as lizards vary widely in their degree of sexual dimorphism, and the role of sexual dimorphism in sex-based microbiome differences could be explicitly tested in this group. Similarly, the roles of body size, age, and life stage in shaping microbial diversity and composition are poorly resolved across taxa and ecological contexts, and patterns of phyllosymbiosis remain inconsistent. Although reproductive behavior appears to modulate microbiomes, its generality across species and functional consequences for hosts are largely unknown. Studies have broadly observed environmental influences, but because single variables have been tested in isolation, it is difficult to disentangle interacting effects of multiple environmental pressures. Moreover, while captivity and urbanization clearly remodel gut communities, their consequences for host physiology and fitness remain unexplored.

Emerging evidence links the microbiome to host traits such as growth, thermal tolerance, metabolic rate, and immune function, but most findings have been correlative thus far. Mechanistic, controlled experiments are needed to establish causality and identify specific microbial taxa or metabolites driving phenotypic outcomes (Amato et al. 2019). Approaches such as probiotic supplementation, fecal transplants, antibiotic treatments, and dietary interventions can be useful tools for future studies to establish mechanistic links. Progress has also been limited by the lack of a standardized model lizard system—such as one with germ-free individuals—that would allow for controlled manipulation of host genetics, microbial composition, and environment (Douglas 2019, Uzbay 2019).

Advancing the field will require integrative, comparative research across ecological contexts to clarify how intrinsic and extrinsic factors interact to shape microbiomes (Williams and Fontaine 2024). This should involve longitudinal sampling, experimental manipulations, and multi-omics analyses to not only elucidate the influence of the microbiome in lizard trait expression but also provide a foundation for conservation applications linking environmental stressors, microbiomes, and host biology (Bahrndorff et al. 2016, Jin Song et al. 2019).

## Conclusions

Research on lizard microbiomes is rapidly growing and is beginning to show that microbial communities are not merely passengers but integral components of lizard ecology and physiology. Because lizards span an exceptional range of evolutionary histories, ecological strategies, and local environments, they offer a powerful comparative system for examining how host-microbe relationships emerge and change. As ectotherms whose physiology is tightly coupled to environmental conditions, lizards are also uniquely positioned to inform how climate, habitat alteration, and other stressors reshape host-microbiome interactions—questions of growing urgency under global environmental change. The integration of microbiome research into studies of lizards has the potential not only to transform our understanding of lizard biology but also to contribute more generally to theory on host-microbe interactions and their role in mediating organismal responses to environmental change, positioning lizards as valuable models at the interface of microbiology, ecology, evolution, and conservation biology.

## Funding

SSF was supported by the NSF PRFB award number 2208809. CEW was supported by a Smithsonian Tropical Research Institute Pre-doctoral Fellowship.

## Supplementary material

Supplementary material are available at [FEMSLE](https://femsle.org) online.

## Conflicts of interest

None declared

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