Journal of Helminthology

www.cambridge.org/jhl

Research Paper

Cite this article: Teixeira AAM, Brito SV, Ribeiro SC, Yamada FH, Almeida WO and Mesquita DO (2026). An expanded species–area perspective on helminth diversity and infection load in lizards: A phylogenetic comparative approach. *Journal of Helminthology*, **100**, e45, 1–8
https://doi.org/10.1017/S0022149X26101448

Received: 29 October 2025
Revised: 25 March 2026
Accepted: 26 March 2026

Keywords:
Host-parasite interactions; phylogenetic comparative methods; phylogenetic signal; host body size; parasite load

Corresponding author:
A.A.M. Teixeira;
Email: adoniasteixeira01@gmail.com

An expanded species–area perspective on helminth diversity and infection load in lizards: A phylogenetic comparative approach

A.A.M. Teixeira[1], S.V. Brito[2], S.C. Ribeiro[1], F.H. Yamada[1], W.O. Almeida[1] and D.O. Mesquita[3]

[1]Programa de Pós-graduação em Diversidade Biológica e Recursos Naturais (PPGDR), Universidade Regional do Cariri – URCA, Rua Cel, Antônio Luiz, 1161, Campus Pimenta, CEP, Crato, CE, Brazil; [2]Centro de Ciências de Chapadinha, Universidade Federal do Maranhão, BR-222, Km 04, S/N, Boa Vista, CEP, Chapadinha, MA, Brazil and [3]Programa de Pós-Graduação em Ciências Biológicas (Zoologia), Departamento de Sistemática e Ecologia, Centro de Ciências Exatas e da Natureza, Universidade Federal da Paraíba, Cidade Universitária, Campus I, CEP, João Pessoa, PB, Brazil

Abstract

Hosts function as ecological islands for endoparasites, offering structured habitats that support parasite survival, growth, and reproduction. Larger and older hosts are often expected to harbour more diverse and abundant parasitic assemblages due to increased structural complexity and longer exposure times. In this study, we investigated how host body size and phylogenetic relatedness influence endoparasite mean richness and mean intensity of infection in lizards from the Atlantic Rainforest of northeastern Brazil. We analysed 121 parasitised specimens representing 15 species, recording body size metrics (SVL and mass) and calculating parasitological indices. Significant phylogenetic signal was detected for host body size (SVL and mass) and mean intensity of infection, whereas no phylogenetic signal was found for mean parasite richness. Contrary to the island theory predictions, PGLS models revealed a significant negative relationship between mean SVL/mass and mean intensity of infection. Furthermore, no significant relationship was found between host body size (SVL or mass) and mean parasite richness, regardless of the evolutionary model used. The pPCA identified a predominance of global structure (phylogenetic relatedness), explaining 42.15% of the variation, while local structures, reflecting niche differentiation, accounted for 18.61%. Our results demonstrate that lizard–parasite interactions are shaped by a complex synergy between conserved evolutionary templates and opportunistic ecological responses, highlighting the necessity of integrated phylogenetic approaches in parasitological studies.

Introduction

Hosts provide essential biological conditions and resources for parasites, with endoparasite dispersal being primarily constrained by host movement and specific transmission pathways (Krasnov et al. 2002; Patterson and Ruckstuhl 2013; Perlin et al. 2025; Poulin 2007). Under the island biogeography framework, host structure and age are key determinants of parasite assemblages (Kuris et al. 1980). Larger hosts, characterised by increased tissue complexity and greater surface area, offer a wider range of colonisation sites and resources, which promotes niche differentiation and facilitates parasite coexistence (Doña and Johnson 2023; Fisher et al. 2020; Kamiya et al. 2014; Oliveira et al. 2022).

Complementing this structural role, body size increases the probability of parasite encounters, either through the entry of monoxenous larvae or the ingestion of heteroxenous species via higher prey consumption (Benesh et al. 2021; Rasmussen and Randhawa 2018). Furthermore, older individuals often exhibit higher parasite loads due to cumulative exposure over time (Cunha-Barros et al. 2003). While these ecological drivers are well-documented, the relative influence of host evolutionary history on these patterns remains a critical area for investigation.

These theoretical predictions find strong empirical support in squamate reptiles. Lizards, in particular, serve as valuable models for studying parasitic systems, with several studies, particularly within the Tropiduridae (Anjos et al. 2012; Silva et al. 2023) and Teiidae families (Ramírez-Morales et al. 2012; Ribas et al. 1998), demonstrating a positive association between host size and parasite load. Conversely, the limiting role of small body size is evident in various Gymnophthalmidae species (Oliveira et al. 2017; Ribeiro et al. 2018; Teixeira et al. 2018b). However, because the ecological traits and phylogenetic relationship patterns of these hosts are often inherited from common ancestors, data from related species cannot be treated as statistically independent (Felsenstein 1984; Garamszegi 2014). Consequently, the complexity of these host-parasite interactions requires phylogenetic comparative methods to disentangle the contribution of evolutionary and ecological factors, ensuring that observed patterns reflect contemporary processes rather than mere shared ancestry (Brooks and McLennan 1991; Harvey and Pagel 1991).

Furthermore, the relative influence of these factors may vary according to parasite life-history strategies. While monoxenous parasites are primarily affected by environmental conditions such as temperature and humidity, heteroxenous species depend on the availability of suitable intermediate hosts for transmission (Anderson 2000; Schmid-Hempel 2021). Such distinct life cycles suggest that different responses might be expected among parasite groups, further justifying a detailed investigation of these drivers (Martins and Poulin 2024).

Therefore, we used endoparasite data from lizards collected during field expeditions in the Atlantic Rainforest of northeastern Brazil, representing the ecological and phylogenetic diversity of the local lizard assemblages, to investigate the relative influence of ecological and historical factors on the widely documented relationship between lizard body size and mass and the richness and intensity of infection of endoparasites. Here, historical factors are understood as the combined outcomes of long-term processes that shape and transmit inherited traits among species, while ecological factors represent more recent influences that modify the organisation of host assemblages (Ricklefs and Miller 1999). Considering that host phylogeny directly influences the diversification of parasite life-history strategies, we hypothesise that variation in parasite diversity and load among lizard hosts is shaped by a combination of ecological and phylogenetic relationships, highlighting the importance of phylogenetic approaches to understanding the ecological and evolutionary processes driving these interactions.

Materials and Methods

Dataset

Sampling was conducted in six areas of the Atlantic Rainforest, in the state of Paraíba, Northeast Brazil. For a detailed description of the collection sites, specimen capture methodology, and endoparasite identification process, see Teixeira et al. (2020, 2025). After euthanasia, all lizards had their snout-vent length (SVL, mm) and mass (g) measured. Because these two metrics are widely treated as distinct life-history traits in studies addressing life-history patterns of lizards (Mesquita et al. 2016a), both were retained for the analyses. We assessed the association between SVL and body mass using Pearson's product–moment correlation, and these variables were subsequently used in separate sets of models. For all analyses, species-level averages were calculated for each trait.

We recorded parasite abundance (the total number of parasites, regardless of species, in a single infected host) and parasite richness (the total number of parasite species per host specimen) following Bush et al. (1997). To incorporate this data into phylogenetic comparative analyses, we then calculated the mean intensity of infection (the total number of parasites across all infected hosts, divided by the number of infected hosts) and mean parasite richness (the mean number of parasite species) for each infected lizard species.

Phylogeny and Statistical Analyses

All statistical analyses were conducted using R Statistical Software v4.4.2 (R Core Team 2024). Throughout the text, means are presented as ±1 standard deviation (SD), and the significance level for hypothesis tests was set at 5%. From a time-calibrated tree for Squamata (Title et al. 2024), we pruned the branches to ensure that our trees included only the taxa present in the studied assemblage.

We assessed the phylogenetic signal using *Bloomberg's K* (Blomberg et al. 2003) and *Pagel's λ* (Pagel 1997, 1999) using the *phylosig* function in the *phytools* package (Revell 2012). All variables were transformed using Log10 $(x + 1)$ prior to analysis. Values of K and λ close to 0 indicate phylogenetic independence, whereas values near 1 suggest that species' traits follow a Brownian motion model of evolution (Blomberg et al. 2003; Freckleton et al. 2002; Losos 2008; Pagel 1999). Additionally, K values greater than 1 indicate that closely related species are more similar than expected under a Brownian motion model of trait evolution (Blomberg et al. 2003; Münkemüller et al. 2012). The significance of the phylogenetic signal detected by K was tested using 1,000 randomisations of species names within the phylogeny (Blomberg et al. 2003). For λ, significance was assessed using a likelihood ratio test (Pagel 1999), comparing the likelihood of the observed λ to that of $\lambda = 1$. Both metrics were employed to ensure a more robust evaluation, as they offer complementary sensitivities to different evolutionary patterns and phylogenetic tree structures (Münkemüller et al. 2012).

To examine the relationships between host morphology and parasitological indices, we performed Phylogenetic Generalised Least Squares (PGLS) models. Specifically, we evaluated the influence of mean SVL and mean mass on both mean intensity of infection and mean parasite richness. These models were implemented based on the Brownian Motion (BM) model and Pagel's λ model. The BM model describes the evolution of continuous traits under random drift or adaptive evolution tracking randomly shifting optima for each lineage (Cavalli-Sforza and Edwards 1967), whereas Pagel's λ model adjusts the analysis to account for phylogenetic dependence, ranging from complete independence ($\lambda = 0$) to the dependence expected under a constant-variance (Brownian motion) model ($\lambda = 1$). The optimal value of λ was estimated using Maximum Likelihood (ML) to ensure the most robust fit for each variable. (Freckleton et al. 2002).

In addition, PGLS models were performed independently for heteroxenous or monoxenous parasite taxa to account for potential differences in infection drivers related to parasite life cycles. For variables that did not meet normality assumptions (e.g., mean richness), we exclusively employed Pagel's λ model estimated via Maximum Likelihood (ML). By using ML estimation, we ensured that the degree of phylogenetic correction (based on the host phylogeny) was tailored to the specific distribution of infection data within each parasite category. This approach provides a more robust assessment of host-parasite associations even under non-normal residual distributions (Freckleton et al. 2002; Pagel 1999; Revell 2012).

To further investigate the potential influence of ecological and historical factors on endoparasite assemblages, we performed a Phylogenetic Principal Component Analysis (pPCA) using the *adephylo* package. This multivariate approach assesses phylogenetic autocorrelation (Gittleman and Kot 1990) by incorporating two distinct matrices: matrix X, which contained the mean intensity of infection for each parasite taxon (representing the parasitological traits under study), and matrix W, a proximity matrix derived from the host's phylogenetic distances to account for shared ancestry. The objective was to identify combinations of parasite infection patterns that exhibit significant variance and display either global or local structures. In this context, global structures would indicate that parasite intensity is strongly associated with the host's deeper evolutionary lineages (high phylogenetic signal) (Winemiller and Pianka 1990), whereas local structures would suggest that differences in parasite load are driven by recent divergences or specific ecological shifts among closely related host species (Jombart et al. 2010).

In this analysis, global and local structures are reflected by positive and negative eigenvalues, respectively (Jombart et al. 2010). Finally, to identify the statistically significant variables that most strongly impact both the Global and Local 1st PCs (either positively or negatively), we performed a Monte Carlo test with 1,000 randomisations.

Results

The final study sample comprised 121 parasitised individuals across 15 lizard species (Table 1), following the refinement of the original dataset from Teixeira et al. (2020). These 15 species formed the basis of the phylogenetic reconstruction used in subsequent comparative analyses (Figure 1). A total of 1,338 endoparasites were identified, representing 14 taxa, including 11 nematodes, one trematode, one cestode, and one acanthocephalan (Table 2). Given the focus on parasitised specimens, the resulting data reflects the composition and load within infected hosts rather than population-level prevalence.

No phylogenetic signal was found for mean parasite richness (Blomberg's $K = 0.48$, $P = 0.21$; Pagel's $\lambda = 0$, $P < 0.001$). The significant p-value for λ confirms a significant departure from the Brownian Motion model ($\lambda = 1$), rather than the presence of phylogenetic dependence. All other parameters showed significant phylogenetic signal for both Blomberg's K and Pagel's λ (Table 3). Mean SVL and mean mass were strongly correlated across species ($r = 0.974$, $P < 0.001$), and each trait exhibited detectable phylogenetic signal. For this reason, we analysed the traits in parallel but never within the same model.

Table 1. Lizards collected in the Atlantic Rainforest, northeastern Neotropical region

	N°	SVL ± SD	Mass ± SD
Family Anguidae			
Diploglossus lessonae	2	131.02	34.9
Family Dactyloidae			
Anolis fuscoauratus	7	38.79 ± 7.12	1.44 ± 0.73
Anolis ortonii	6	41.6 ± 9.88	1.7 ± 0.9
Anolis punctatus	38	70.16 ± 12.56	6.29 ± 2.51
Family Gymnophthalmidae			
Dryadosaura nordestina	97	37.99 ± 10.55	1.08 ± 0.71
Family Leiosauridae			
Enyalius bibronii	1	95.13	23
Enyalius catenatus	5	85.05 ± 7.81	19.2 ± 4.83
Family Mabuyidae			
Copeoglossum nigropunctatum	7	88.54 ± 19.1	17.08 ± 7.54
Psychosaura agmosticha	9	67.15 ± 2.77	6.03 ± 1.09
Family Phyllodactylidae			
Gymnodactylus darwinii	14	42.23 ± 12.58	2.17 ± 1.6
Family Sphaerodactylidae			
Coleodactylus meridionalis	88	23.27 ± 2.02	0.25 ± 0.07
Family Teiidae			
Ameiva ameiva	13	68.8 ± 23.2	11.49 ± 11.8
Kentropyx calcarata	135	55.2 ± 16.22	6.31 ± 6.63
Family Tropiduridae			
Strobilurus torquatus	20	58.46 ± 11.54	7.22 ± 3.79
Tropidurus hispidus	10	63.2 ± 20.97	11.64 ± 10.26

N°: number of analysed host; SVL: mean snout-vent length; SD: standard deviation.

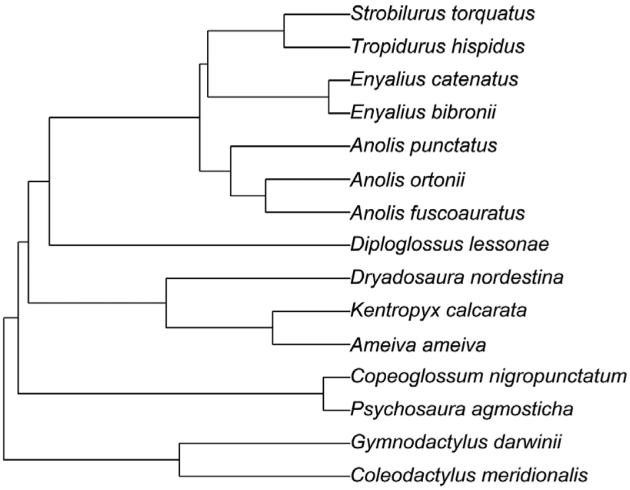

Figure 1. Phylogeny obtained from Title et al. (2024), including only the parasitised lizard species from our sampling.

Regarding the influence of host size (mean SVL) on the mean intensity of infection (the response variable), both models showed a significant negative relationship: BM model (adjusted R^2: 0.27; F-statistic: 6.40; b1: –1.42; AIC: 14.14; P-value: 0.02) and Lambda model (adjusted R^2: 0.21; F-statistic: 4.87; b1: –1.28; AIC: 14.63; P-value: 0.04). For the relationship between mean mass and mean intensity of infection (the response variable), only the BM model yielded a significant negative relationship (adjusted R^2: 0.21; F-statistic: 4.886; b1: –0.42; AIC: 15.36; P-value: 0.04), whereas the Lambda model was not significant (adjusted R^2: 0.13; F-statistic: 3.141; b1: –0.35; AIC: 16.16; P-value: 0.09).

No significant relationship was found between mean SVL and mean parasite richness (the response variable) for Lambda model (adjusted R^2: –0.063; F-statistic: 0.162; b1: –0.08; AIC: –15.89; P-value: 0.693); or between mean mass and mean parasite richness (the response variable) for Lambda model (adjusted R^2: –0.074; F-statistic: 0.034; b1: –0.07; AIC: 34.51; P-value: 0.856). When analysed independently by transmission mode, the influence of mean SVL and mean mass on both mean intensity of infection and mean parasite richness was not significant for either heteroxenous or monoxenous parasites (see Supplementary Material).

Both global and local structures were identified by pPCA in the endoparasite data. However, global structure (phylogenetic relationship) had a stronger influence on infection patterns in lizards, as positive eigenvalues (0.031) were considerably higher than negative eigenvalues (–0.013).

In the first Global component (PC1 Global), the lizard species *Ameiva ameiva* and *Kentropyx calcarata* (Teiidae) had the most positive scores, while *Strobilurus torquatus* had the most negative score (Figure 2). The variables significantly influencing PC1 Global were the nematode *Pharyngodon sp.* (P-value: 0.026) and the cestode *Oochoristica sp.* (P-value: 0.037), with the highest positive loadings of 0.75 and 0.51, respectively. The taxa with the most negative loadings were the nematode *Strongyluris oscari* (–0.25; P-value: 0.20) and the trematode *Haplometroides odhneri* (–0.11;

Table 2. Composition of helminths from the Atlantic Rainforest, infected hosts, mean intensity of infection (MII), and sites of infection (SI)

Parasite	Host	MII ± SD	SI
ACHANTHOCEPHALA			
Family Oligacanthorhynchidae			
Oligacanthorhynchus sp.	*Ameiva ameiva*	1	LI
	Coleodactylus meridionalis	1.2 ± 0.5	S, CC
CESTODA			
Family Anoplocephalidae			
Oochoristica sp.	*Ameiva ameiva*	2	LI
	Kentropyx calcarata	19.2 ± 6.4	S, SI, LI
	Tropidurus hispidus	1	LI
NEMATODA			
Family Cosmocercidae			
Aplectana sp.	*Gymnodactylus darwinii*	1	SI, LI
	Dryadosaura nordestina	9.4 ± 8.4	S, SI, LI
	Diploglossus lessonae	1	LI
	Anolis fuscoauratus	2	L
	Enyalius catenatus	1	LI
Cosmocerca sp.	*Dryadosaura nordestina*	11.2 ± 7.7	LI
Family Heterakidae			
Strongyluris oscari	*Anolis fuscoauratus*	9	S, SI
	Anolis punctatus	7	S, LI
	Tropidurus hispidus	3	S, SI
	Strobilurus torquatus	17	LI
Family Onchocercidae			
Piratuba sp.	*Kentropyx calcarata*	1	LI
Family Pharyngodonidae			
Pharyngodon sp.	*Ameiva ameiva*	29.5	LI
	Kentropyx calcarata	9	S
Parapharyngodon alvarengai	*Tropidurus hispidus*	3.3 ± 2	SI
Spauligodon loboi	*Strobilurus torquatus*	13	SI, LI
Family Physalopteridae			
Physaloptera lutzi	*Coleodactylus meridionalis*	12.5	S, SI
	Dryadosaura nordestina	12 ± 4.8	S
	Anolis ortonii	1	S
	Anolis punctatus	4	LI
	Strobilurus torquatus	10.6	S, SI
Physaloptera retusa	*Copeoglossum nigropunctatum*	1	S
	Kentropyx calcarata	5	S
	Enyalius bibronii	3	S
	Tropidurus hispidus	5.3 ± 6.6	S, SI
Family Rabdiasidae			
Rhabdias sp.	*Anolis ortonii*	1	L
	Enyalius catenatus	5	L
Family Seuratoidae			
Skrjabinellazia intermedia	*Anolis fuscoauratus*	5	S
	Anolis punctatus	1	SI
TREMATODA			
Family Plagiorchiidae			
Haplometroides odhneri	*Coleodactylus meridionalis*	1.5	S
	Psychosaura agmosticha	3	S
	Dryadosaura nordestina	3.5 ± 2.6	S, SI, LI
	Anolis ortonii	16	S
	Anolis punctatus	3	SI
	Tropidurus hispidus	1	LI

S: stomach; SI: small intestine, LI: large intestine, L: lungs, CC: celomatic cavity.

Table 3. Estimates of phylogenetic signal in host body size and endoparasite infection parameters for lizard species from the Atlantic Rainforest, Brazil. P-values for Pagel's λ reflect the likelihood ratio test against the Brownian Motion model ($\lambda = 1$)

Variable	Blomberg's *K*	P-value	Pagel's λ	P-value
mean SVL	0.66	**0.03**	0.93	**<0.001**
mean mass	0.69	**0.04**	0.95	**0.01**
mean intensity of infection	0.76	**0.01**	0.88	**0.01**
mean parasite richness	0.48	0.21	0	**<0.001**

P-value: 0.87), though these variations were not statistically significant (Figure 3).

In the first Local component (PC1 Local), *S. torquatus* and *A. ameiva* had the most negative scores, while *K. calcarata* had the highest positive score (Figure 2). The endoparasites most influencing PC1 Local were *Pharyngodon sp.* (–0.58; P-value: 0.028) and *S. oscari* (–0.15; P-value: 0.15), with only *Pharyngodon sp.* showing a statistically significant variation. Conversely, *Physaloptera retusa* (0.25; P-value: 0.503) and *Oochoristica sp.* (0.73; P-value: 0.038) had the highest positive loadings, with only *Oochoristica sp.* being statistically significant (Figure 3).

Discussion

Quantitative Traits and Phylogenetic Signal

As expected, mean SVL and body mass exhibited a strong phylogenetic signal (Table 3), confirming that body size is a highly conserved trait across the studied lizard lineages (Cavalcanti et al. 2023; Diaz-Ortega et al. 2024; Mesquita et al. 2016b). This morphological conservatism is relevant to our findings because host body size often dictates the available space and resource diversity for parasite colonisation

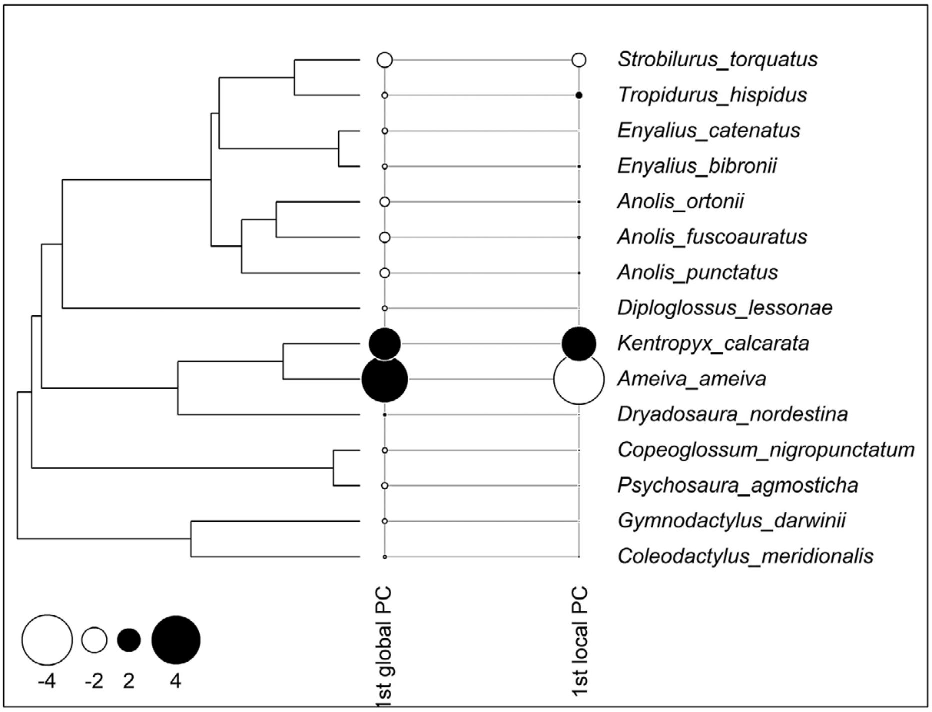

Figure 2. Phylogenetic tree and scatter plot of the phylogenetic Principal Component Analysis (pPCA) of the mean intensity of infection in the lizard assemblage from the Atlantic Rainforest, northeastern Brazil. Black circles: positive autocorrelation; white circles: negative autocorrelation in PC1 Global and PC1 Local.

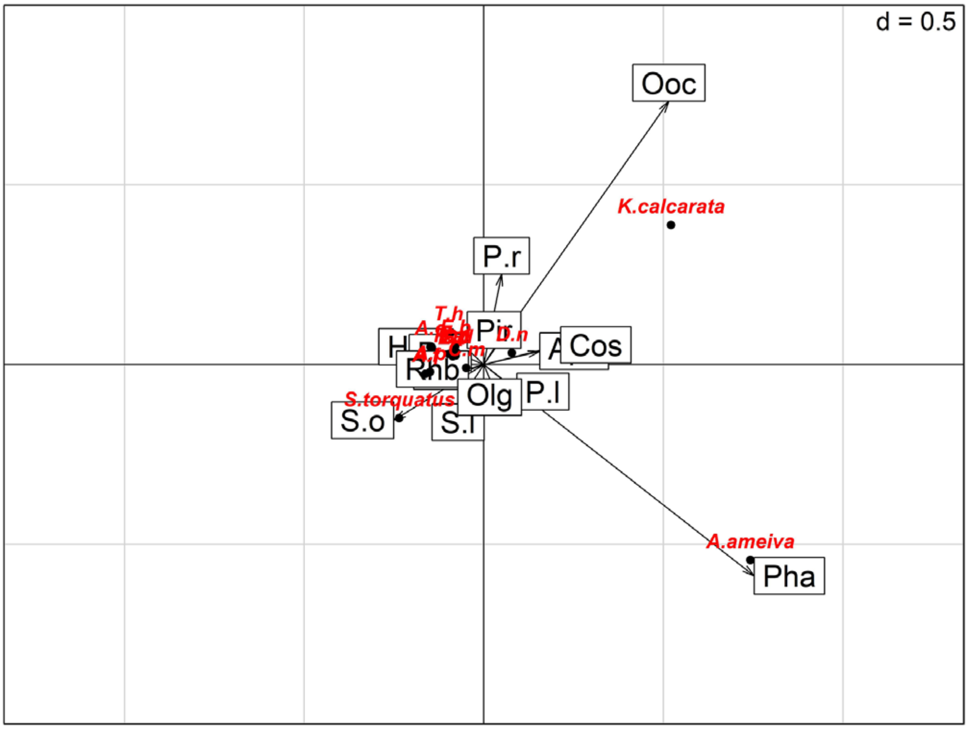

Figure 3. Loadings of mean intensity of infection for each parasite taxon concerning the global axis (horizontal) and local axis (vertical). The lizard species composing the studied assemblage were plotted in the Cartesian plane. Legend: *Physaloptera lutzi* (P.l); *Physaloptera retusa* (P.r); *Strongyluris oscari* (S.o); *Spauligodon loboi* (S.l); *Aplectana* sp. (Apc); *Haplometroides odhneri* (H.o); *Skrjabinellazia intermedia* (S.i); *Cosmocerca* sp. (Cos); *Parapharyngodon alvarengai* (P.a); *Oochoristica* sp. (Ooc); *Rhabdias* sp. (Rhb); *Oligacanthorhynchus* sp. (Olg); *Pharyngodon* sp. (Pha); *Piratuba* sp. (Pir).

(Perlin et al. 2025). By maintaining predictable physical characteristics over evolutionary time, these host lineages have historically provided stable environments capable of influencing the patterns of intensity observed in this assemblage (Kamiya et al. 2014; Martins et al. 2024).

Beyond host body size, the mean intensity of infection also exhibited a phylogenetic signal close to 1 (Table 3). Rather than reflecting host tolerance alone, this pattern suggests a significant degree of phylogenetic conservatism in host susceptibility or exposure levels within this assemblage. This indicates that closely related lizard species tend to harbour similar parasite loads, a phenomenon that may be linked to shared physiological or behavioural constraints inherited from common ancestors (Perlin et al. 2025; Poulin and Mouillot 2005). While ecological factors undeniably trigger infection events, the strong phylogenetic signal suggests that evolutionary history provides a fundamental template that shapes the intensity of these interactions in the studied hosts.

From an ecological standpoint, infection rates can vary among host species due to several factors, such as feeding habits, foraging strategies, seasonal changes, population density, and ecological interactions (Brito et al. 2014b; Teixeira et al. 2021). However, our results suggest that an evolutionary perspective is equally essential, as phylogenetic relationships between hosts appear to determine their underlying patterns of susceptibility. Phylogenetically related hosts share physiological barriers and immune profiles that facilitate the transition of related parasites across lineages without requiring major evolutionary leaps (Perlin et al. 2025). Furthermore, a parsimonious explanation for these patterns is that closely related hosts often share the same parasite species, as past co-evolutionary history typically dictates which realised interactions are possible. In this context, infection intensity may also be interpreted as a trait of the parasite itself, which remains consistently expressed across phylogenetically similar host environments (Poulin 2010). Conversely, greater phylogenetic distance acts as a robust barrier; more divergent biological responses necessitate larger adaptive jumps for successful colonisation, effectively limiting shared parasite loads across the assemblage (Schmid-Hempel 2021).

Unlike other traits, mean parasite richness showed no significant phylogenetic signal, suggesting that, for this variable, contemporary ecological factors may be more influential than historical heritage at the studied scale. This lack of phylogenetic structure may be explained by the ‘encounter filter’ (Combes 2001), which is highly sensitive to local environmental conditions. Consequently, the observed richness likely reflects adaptive adjustments to immediate ecological opportunities rather than conserved evolutionary lineages.

In the Atlantic Forest, habitat fragmentation has been shown to alter parasite infection patterns by modifying host diet and prey availability. For instance, larger fragments often support a higher richness of heteroxenous helminths due to greater intermediate host diversity (Teixeira et al. 2021). Furthermore, the low prevalence and richness observed in some Atlantic Forest lizard populations highlight how local environmental degradation in fragmented landscapes may influence the stability of parasite-host interactions, potentially leading to lower richness levels than those expected for more preserved tropical ecosystems (Teixeira et al. 2018a). These findings suggest that environmental disturbance may obscure or overlay the ancestral patterns of parasite diversity in this assemblage, potentially making historical signals more difficult to detect.

Relationship Between Morphological Traits and Parasitic Rates

We predicted that the mean intensity of infection would be positively correlated with lizard size and mass. However, most tests revealed significant inverse trends. Larger lizards were expected to host more endoparasites due to their larger body size, greater space, more nutritional resources (Ávila et al. 2010; Kuris et al. 1980; Oliveira et al. 2017; Teixeira et al. 2018b), and larger body surface area for infection (Rasmussen and Randhawa 2018).

This inverse relationship aligns with the findings of George-Nascimento et al. (2004), who observed that larger vertebrate hosts often exhibit lower mean infection intensities due to metabolic constraints. While smaller hosts may face stronger selection pressures against heavy infections, larger species might ‘dilute’ these rates, potentially reducing the selective pressure per individual parasite. Although such patterns can be driven by parasite traits, such as life-cycle complexity (e.g. monoxenous vs. heteroxenous) (Martins and Poulin 2024), our separate analyses for these groups yielded no significant results. This suggests that the observed pattern in this assemblage is more likely a reflection of host-specific constraints or a cumulative community-level effect rather than being driven by specific parasite life-history strategies. Nevertheless, the lack of a significant signal for richness suggests that ecological factors still play a role, even if evolutionary history remains a strong predictor for infection intensity.

Diverging from the patterns observed for infection intensity, parasite richness showed no association with SVL or body mass, even when accounting for phylogeny. While parasite richness is often expected to exhibit phylogenetic structuring due to conserved host physiological traits and long-term co-evolutionary dynamics (Kamiya et al. 2014), our results suggest that these evolutionary constraints may be overridden by contemporary ecological drivers in this system. However, it is important to consider that richness metrics can be highly sensitive to sampling bias and the ‘encounter filter’ (Combes 2001). Therefore, the lack of a significant signal in our study does not necessarily imply that phylogeny is generally unimportant for parasite accumulation; rather, it suggests that local anthropogenic or environmental changes in the ecosystem may disrupt or obscure expected evolutionary patterns (Malagon and Bernal 2018).

This ecological dominance is further supported by studies in the Atlantic Forest, where Teixeira et al. (2018a) observed remarkably low helminth infection rates in *K. calcarata* populations. Such patterns likely reflect the severe fragmentation of this ecosystem, which is now reduced to less than 8% of its original cover (Tabarelli and Santos 2004). This environmental degradation profoundly affects invertebrate and plant assemblages (Pimm and Raven 2000), subsequently disrupting the availability of intermediate hosts. These anthropogenic changes may provide a partial explanation for the lack of phylogenetic signal in parasite richness. Our findings highlight the potential for habitat disturbance to disrupt well-established ecological relationships, including the influence of microhabitat and prey availability on parasite communities (Brito et al. 2014a).

Relevance of Ecological and Phylogenetic relationship

Our results indicate that a substantial portion of the variation in the lizard-parasite assemblage is structured by global components, with PC1 Global explaining 42.15% of the variation, while the local component (PC1 Local) accounted for 18.61%. In the pPCA framework, global structures reflect variables with strong phylogenetic autocorrelation, suggesting that certain infection patterns are deeply anchored in the host’s evolutionary lineages. This suggests that the shared ancestry of these lizards provides a consistent template for parasite interactions (Brooks and McLennan 1991) reflecting historical co-evolutionary processes within the Atlantic Forest, the signals of which may persist in traits like infection intensity despite contemporary environmental disturbances.

In contrast, the local component represents patterns where closely related species differ more than expected by chance, likely reflecting niche differentiation or opportunistic responses to immediate environmental conditions. Rather than a strict dichotomy between history and ecology, these findings demonstrate that while most life-history traits in this assemblage are phylogenetically conserved, a smaller but relevant portion of the variation is driven by specific ecological adjustments. Following Jombart (2010), this integrated approach allows us to identify how evolutionary constraints and ecological plasticity together shape the structural patterns of infection across the lizard assemblage.

Species such as *K. calcarata* and *A. ameiva* (Teiidae) exerted a substantial influence on both global and local axes, correlating with the parasites *Oochoristica* sp. and *Pharyngodon* sp., respectively. Although both are active foragers, their distinct microhabitat preferences, with the former inhabiting humid forest interiors and the latter restricted to open areas and edges, likely explain their differing dietary breadths and parasite associations (Franzini et al. 2019; Vitt and Colli 1994). These ecological differences are further reflected in parasite transmission dynamics, as heteroxenous species like *Oochoristica* sp. are influenced by both global and local factors due to their reliance on intermediate host availability, whereas monoxenous parasites such as *Pharyngodon* sp. are primarily shaped by environmental conditions like temperature and humidity (Anderson 2000). This variation underscores the intricate interplay between host ecology and parasite life-cycle strategies in determining infection patterns across the assemblage.

In conclusion, our study demonstrates that while host morphology is highly conserved, its influence on helminth communities is complex and trait-dependent. The strong phylogenetic signal observed for infection intensity suggests that evolutionary history provides a fundamental template for host susceptibility, potentially driven by shared physiological constraints or the inheritance of specific parasite lineages. Conversely, the lack of phylogenetic structure in parasite richness highlights the dominance of contemporary ecological filters and habitat disturbance in the Atlantic Forest, which may obscure ancestral patterns of diversity. By integrating phylogenetic and ecological perspectives, these findings provide a more comprehensive understanding of the mechanisms governing host-parasite interactions in changing tropical landscapes.

Supplementary material. The supplementary material for this article can be found at http://doi.org/10.1017/S0022149X26101448.

Acknowledgements. We thank the Fundação Cearense de Apoio ao Desenvolvimento Científico e Tecnológico (FUNCAP) for the research fellowship granted to AAMT (PVS-0215-00125.01.00/23). We also acknowledge the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for research fellowships awarded to WOA (PQ-308534/2021-2) and FHY (304502/2022-7 and 174814/2023-2). Additionally, DOM thanks CNPq and FAPESQ-PB for a PRONEX fellowship (Edital 6/2018). We are grateful to all members of the Laboratório de Vertebrados e Paleontologia-DCB (UFPB-Campus II), Núcleo de Ecologia de Serpentes-NES (UFPB-Campus IV), and the Curupira Republic Family. We also acknowledge the assistance of the employees of RPNN-EG and BMBG.

Financial support. None.

Competing interests. None.

Ethical standard. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. Research was permitted by Biodiversity Authorization and Information System of the Brazilian Institute of Environment and Renewable Natural Resources (no. 54378/3, authentication code 78752298; no. 56863-1, authentication code 47783645), Committee of the Superintendence of Environmental Management (no. 004/2016, process no. 5376/16), and Benjamim Maranhão Botanical Garden-BMBG (no. 003/2016/).

References

Anderson RC (2000) *Nematode Parasites of Vertebrates: Their Development and Transmission*, 2nd edn. New York, CABI Publishing.

Anjos LA, **Ávila RW**, **Ribeiro SC**, **Almeida WO and Silva RJ** (2012) Gastrointestinal nematodes of the lizard *Tropidurus hispidus* (Squamata: Tropiduridae) from a semi-arid region of northeastern Brazil. *Journal of Helminthology* **81**, 443–449.

Ávila RW, **Anjos LA**, **Gonçalves U**, **Freire EMX**, **Almeida WO and Silva RJ** (2010) Nematode infection in the lizard *Bogertia lutzae* (Loveridge, 1941) from the Atlantic forest in north-eastern Brazil. *Journal of Helminthology* **84**, 199–201. doi:10.1017/S0022149X09990538.

Benesh DP, **Parker G and Chubb JC** (2021) Life-cycle complexity in helminths: What are the benefits? *Evolution* **75**, 1936–1952. doi:10.1111/evo.14299.

Blomberg SP, **Garland Jr, T and Ives AR** (2003) Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* **57**, 717–745. doi:10.1111/j.0014-3820.2003.tb00285.x.

Brito SV, **Corso G**, **Almeida AM**, **Ferreira FS**, **Almeida WO**, **Anjos LA**, **Mesquita DO and Vasconcellos A** (2014a) Phylogeny and micro-habitats utilized by lizards determine the composition of their endoparasites in the semiarid Caatinga of Northeast Brazil. *Parasitology Research* **113**, 3963–3972. doi:10.1007/s00436-014-4061-z.

Brito SV, **Ferreira FS**, **Ribeiro SC**, **Anjos LA**, **Almeida WO**, **Mesquita DO and Vasconcellos A** (2014b) Spatial-temporal variation of parasites in *Cnemidophorus ocellifer* (Teiidae) and *Tropidurus hispidus* and *Tropidurus semitaeniatus* (Tropiduridae) from Caatinga areas in northeastern Brazil. *Parasitology Research* **113**, 1163–1169. doi:10.1007/s00436-014-3754-7.

Brooks DR and McLennan DA (1991) *Phylogeny, Ecology, and Behavior: A Research Program in Comparative Biology*. Chicago: University of Chicago Press.

Bush AO, **Lafferty KD**, **Lotz JM and Shostak AW** (1997) Parasitology meets ecology on its own terms: Margolis et al. revisited. *The Journal of Parasitology* **83**, 575–583. doi:10.2307/3284227.

Cavalcanti LB.d.Q, **Garda AA**, **Costa TB**, **Savaugere A**, **Pessoa G**, **Colli GR**, **Lion MB and Mesquita DO** (2023) Factors shaping a lizard community structure in a semiarid region of north-eastern Brazil. *Journal of Arid Environments* **219**, 105088. doi:10.1016/j.jaridenv.2023.105088.

Cavalli-Sforza LL and Edwards AWF (1967) Phylogenetic analysis. Models and estimation procedures. *American Journal of Human Genetics* **19**, 233.

Combes C (2001) *Parasitism: The Ecology and Evolution of Intimate Interactions*. Chicago and London: University of Chicago Press.

Cunha-Barros M, **Van Sluys M**, **Vrcibradic D**, **Galdino CAB**, **Hatano FH and Rocha CFD** (2003) Patterns of infestation by chigger mites in four diurnal lizard species from a restinga habitat (Jurubatiba) of Southeastern Brazil. *Brazilian Journal of Biology* **63**, 393–399.

Diaz-Ortega I, **Pérez-Mendoza H**, **Zúñiga-Vega JJ and Flores-Villela O** (2024) Phylogenetic signal of morphological and life-history traits in the genus *Sceloporus*. *Authorea Preprints*. doi:10.22541/au.172114997.72102597/v1.

Doña J and Johnson KP (2023) Host body size, not host population size, predicts genome-wide effective population size of parasites. *Evolution Letters* **7**, 285–292. doi:10.1093/evlett/qrad026.

Felsenstein J (1984) Distance methods for inferring phylogenies: a justification. *Evolution* **38**, 16–24.

Fisher RM, **Shik JZ and Boomsma JJ** (2020) The evolution of multicellular complexity: the role of relatedness and environmental constraints. *Proceedings of the Royal Society B* **287**, 20192963. doi:10.1098/rspb.2019.2963.

Franzini LD, **Teixeira AAM**, **Tavares-Bastos L**, **Vitt LJ and Mesquita DO** (2019) Autecology of *Kentropyx calcarata* (Squamata: Teiidae) in a remnant of Atlantic Forest in Eastern South America. *Journal of Herpetology* **53**, 209–217. doi:10.1670/17-184.

Freckleton RP, **Harvey PH and Pagel M** (2002) Phylogenetic analysis and comparative data: a test and review of evidence. *The American Naturalist* **160**, 712–726. doi:10.1086/343873.

Garamszegi LZ (2014) *Modern Phylogenetic Comparative Methods and Their Application in Evolutionary Biology: Concepts and Practice*. Berlin, Germany: Springer.

George-Nascimento M, **Munoz G**, **Marquet PA and Poulin R** (2004) Testing the energetic equivalence rule with helminth endoparasites of vertebrates. *Ecology Letters* **7**, 527–531. doi:10.1111/j.1461-0248.2004.00609.x.

Gittleman JL and Kot M (1990) Adaptation: statistics and a null model for estimating phylogenetic effects. *Systematic Zoology* **39**, 227–241. doi:10.2307/2992183.

Harvey PH and Pagel MD (1991) *The Comparative Method in Evolutionary Biology*. New York: Oxford University Press.

Jombart T, **Pavoine S**, **Devillard S and Pontier D** (2010) Putting phylogeny into the analysis of biological traits: a methodological approach. *Journal of Theoretical Biology* **264**, 693–701. doi:10.1016/j.jtbi.2010.03.038.

Kamiya T, **O'Dwyer K**, **Nakagawa S and Poulin R** (2014) What determines species richness of parasitic organisms? A meta-analysis across animal, plant and fungal hosts. *Biological Reviews* **89**, 123–134. doi:10.1111/brv.12046.

Krasnov BR, **Khokhlova IS**, **Oguzoglu I and Burdelova NV** (2002) Host discrimination by two desert fleas using an odour cue. *Animal Behaviour* **64**, 33–40. doi:10.1006/anbe.2002.3030.

Kuris AM, **Blaustein AR and Alio JJ** (1980) Hosts as islands. *The American Naturalist* **116**, 570–586.

Losos JB (2008) Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecology Letters* **11**, 995–1007. doi:10.1111/j.1461-0248.2008.01229.x.

Malagon CS and Bernal EV (2018) Competent hosts and endemicity of multi-host diseases. *Quantitative Biology*, arXiv:1705.09426v2 doi:10.48550/arXiv.1705.09426.

Martins ACJS, **Almeida-Santos M**, **Ávila RW**, **Siqueira CC and Rocha CFD** (2024) Does the body size, sex, and reproductive modes of leaf litter anurans affect the diversity of parasites? *Parasitology Research* **123**. doi:10.1007/s00436-024-08266-2.

Martins PM and Poulin R (2024) Universal versus taxon-specific drivers of helminth prevalence and intensity of infection. *Proceedings B* **291**, 20241673. doi:10.1098/rspb.2024.1673.

Mesquita DO, **Costa GC**, **Colli GR**, **Costa TB**, **Shepard DB**, **Vitt LJ and Pianka ER** (2016a) Life-History Patterns of Lizards of the World. *The American Naturalist* **187**, 689–705. doi:10.1086/686055.

Mesquita DO, **Faria RG**, **Colli GR**, **Vitt LJ and Pianka ER** (2016b) Lizard life-history strategies. *Austral Ecology* **41**, 1–5.

Münkemüller T, **Lavergne S**, **Bzeznik B**, **Dray S**, **Jombart T**, **Schiffers K and Thuiller W** (2012) How to measure and test phylogenetic signal. *Methods in Ecology and Evolution* **3**, 743–756. doi:10.1111/j.2041-210X.2012.00196.x.

Oliveira BHS, **Teixeira AAM**, **Queiroz RNM**, **Araujo Filho JA**, **Teles DA**, **Brito SV and Mesquita DO** (2017) Nematodes infecting *Anotosaura vanzolinia* (Squamata: Gymnophthalmidae) from Caatinga, northeastern Brazil. *Acta Herpetologica* **12**, 103–108. doi:10.13128/Acta_Herpetol-18765.

Oliveira CR, **Mascarenhas W**, **Batista-Oliveira D**, **Castro Araújo K**, **Ávila RW and Borges-Nojosa DM** (2022) Endoparasite community of anurans from an altitudinal rainforest enclave in a Brazilian semiarid area. *Journal of Helminthology* **96**, e62. doi:10.1017/S0022149X22000499.

Pagel M (1997) Inferring evolutionary processes from phylogenies. *Zoologica Scripta* **26**, 331–348. doi:10.1111/j.1463-6409.1997.tb00423.x.

Pagel M (1999) Inferring the historical patterns of biological evolution. *Nature* **401**, 877–884. doi:10.1038/44766.

Patterson JEH and Ruckstuhl KE (2013) Parasite infection and host group size: a meta-analytical review. *Parasitology* **140**, 803–813. doi:10.1017/S0031182012002259.

Perlin MH, **Poulin R and de Bekker C** (2025) Invasion of the four kingdoms: the parasite journey across plant and non-plant hosts. *Biological Reviews* **100**, 936–968. doi:10.1111/brv.13169.

Pimm SL and Raven P (2000) Biodiversity: extinction by numbers. *Nature* **403**, 843–845. doi:10.1038/35002708.

Poulin R (2007) *Evolutionary Ecology of Parasites*, 2nd edn. Princeton, New Jersey: Princeton University Press.

Poulin R (2010) Network analysis shining light on parasite ecology and diversity. *Trends in Parasitology* **26**, 492–498. doi:10.1016/j.pt.2010.05.008.

Poulin R and Mouillot D (2005) Combining phylogenetic and ecological information into a new index of host specificity. *The Journal of Parasitology* **91**, 511–514. doi:10.1645/GE-398R.

Ramírez-Morales R, **Lislevand T**, **Retana-Salazar A**, **Solhøy T and Roth S** (2012) Ectoparasite loads of the Central American whiptail lizard *Ameiva festiva* (Squamata: Teiidae). *The Herpetological Journal* **22**, 151–155.

Rasmussen TK and Randhawa HS (2018) Host diet influences parasite diversity: a case study looking at tapeworm diversity among sharks. *Marine Ecology Progress Series* **605**, 1–16. doi:10.3354/meps12751.

R Core Team (2024) *R: A Language and Environment for Statistical Computing*. Vienna, Austria, R Foundation for Statistical Computing.

Revell LJ (2012) phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution* **3**, 217–223. doi:10.1111/j.2041-210X.2011.00169.x.

Ribas SC, **Rocha CFD**, **Teixeira-Filho PF and Vicente JJ** (1998) Nematode infection in two sympatric lizards (*Tropidurus torquatus* and *Ameiva ameiva*) with different foraging tactics. *Amphibia-Reptilia* **19**, 323–330.

Ribeiro LB, **Ferreira ACS**, **Silva DCN**, **Vieira FM and Moura GJB** (2018) Helminth Parasites of the Lizard *Nothobachia ablephara* (Gymnophthalmidae) in Caatinga Areas from the Sertão of Brazil. *The Journal of Parasitology* **104**, 177–182. doi:10.1645/17-90.

Ricklefs RE and Miller GL (1999) *Ecology*, 4th edn. New York: W.H. Freeman Publishers.

Schmid-Hempel P (2021) *Evolutionary Parasitology: The Integrated Study of Infections, Immunology, Ecology, and Genetics*, 2nd edn. Oxford, United Kingdom: Oxford University Press.

Silva GD, **Teixeira AAM**, **Franzini LD**, **Mesquita DO and Brito SV** (2023) A Temporal variation in diet and helminth abundance in the spiny-tailed lizard, Strobilurus torquatus Wiegmann, 1834 (Squamata: Tropiduridae) from the Brazilian Atlantic Forest. *Acta Herpetologica* **18**, 105–114. doi:10.36253/a_h-13767.

Tabarelli M and Santos AMM (2004) Uma Breve Descrição Sobre a História Natural dos Brejos Nordestinos. In Pôrto KC, Cabral JJP and Tabarelli M. (eds), *Brejos de altitude em Pernambuco e Paraíba: História Natural, Ecologia e Conservação*. Brasília, DF, Brasil, Ministério do Meio Ambiente.

Teixeira AAM, **Franzini LD**, **Brito SV**, **Almeida AM and Mesquita DO** (2018a) Very low prevalence of infection by *Physaloptera lutzi* (Nematoda: Physalopteridae) parasitizing *Kentropyx calcarata* (Squamata: Teiidae), from fragments of Atlantic Forest in Northeast Brazil with a summary of nematodes infecting congeneric species. *Herpetology Notes* **11**, 799–804.

Teixeira AAM, **Riul P**, **Brito SV**, **Araujo Filho JA**, **Teles DA**, **Almeida WO and Mesquita DO** (2020) Ecological release in lizard endoparasites from the Atlantic Forest, northeast of the Neotropical Region. *Parasitology* **147**, 491–500. doi:10.1017/S0031182020000025.

Teixeira AAM, **Riul P**, **Brito SV**, **Teles DA**, **Araujo-Filho JA**, **Almeida WO and Mesquita DO** (2025) Are lizard assemblages from the Atlantic Forest under the influence of ecological release? *Austral Ecology* **50**, e70065. doi:10.1111/aec.70065.

Teixeira AAM, **Sampaio NKS**, **Araujo-Filho JA**, **Teles DA**, **Almeida WO**, **Mesquita DO and Brito SV** (2021) Parasitic infection patterns in *Coleodactylus meridionalis* (Squamata: Sphaerodactylidae) from Atlantic Forest fragments, northeast of the Neotropical Region. *Helminthologia* **58**, 356–363. doi:10.2478/helm-2021-0042.

Teixeira AAM, **Silva RJ**, **Brito SV**, **Teles DA**, **Araujo-Filho JA**, **Franzini LD**, **Santana DO**, **Almeida WO and Mesquita DO** (2018b) Helminths infecting *Dryadosaura nordestina* (Squamata: Gymnophthalmidae) from Atlantic Forest, northeastern Brazil. *Helminthologia* **55**, 286–291. doi:10.2478/helm-2018-0026.

Title PO, **Singhal S**, **Grundler MC**, **Costa GC**, **Pyron RA**, **Colston TJ**, **Grundler MR**, **Prates I**, **Stepanova N**, **Jones MEH**, **Cavalcante LBQ**, **Colli GR**, **Di-Poï N**, **Donnellan SC**, **Moritz C**, **Mesquita DO**, **Pianka ER**, **Smith SA**, **Vitt LJ and Rabosky DL** (2024) The macroevolutionary singularity of snakes. *Science* **383**, 918–923. doi:10.1126/science.adh2449.

Vitt LJ and Colli GR (1994) Geographical ecology of a neotropical lizard: *Ameiva ameiva* (Teiidae) in Brazil. *Canadian Journal of Zoology* **72**, 1986–2008. doi:10.1139/z94-271.

Winemiller KO and Pianka ER (1990) Organization in natural assemblages of desert lizards and tropical fishes. *Ecological Monographs* **60**, 27–55. doi:10.2307/1943025.