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RESEARCH ARTICLE

Leveraging Natural History Collections to Understand the Impacts of Global Change

Unwrapping broken tails: Biological and environmental correlates of predation pressure in limbless reptiles

Mario R. Moura[1] | Henrique C. Costa[2] | Arthur D. Abegg[3,4] | Esmeralda Alaminos[5] | Teddy Angarita-Sierra[6] | Weverton S. Azevedo[3,4] | Hugo Cabral[7,8] | Priscila Carvalho[8] | Sonia Cechin[9] | Nathalie Citeli[10] | Ângelo C. M. Dourado[11] | André F. V. Duarte[12] | Frederico G. R. França[13] | Eliza M. X. Freire[12] | Paulo C. A. Garcia[14] | Rafael Mol[15] | Ricardo Montero[16] | Antônio Moraes-da-Silva[17] | Daniel C. Passos[18] | Paulo Passos[19] | Renata Perez[20] | Juan M. Pleguezuelos[21] | Pedro Prado[19] | Ana Lúcia C. Prudente[11] | Raul F. D. Sales[12] | Diego J. Santana[22] | Livia C. Santos[23] | Vinicius T. C. Silva[12] | Vinícius Sudré[19] | Omar Torres-Carvajal[24] | Juan J. Torres-Ramírez[6] | Van Wallach[25] | Gisele R. Winck[26] | Jhonny J. M. Guedes[27]

[1]Departamento de Ciências Biológicas, Universidade Federal da Paraíba, Areia, Brazil; [2]Departamento de Zoologia, Instituto de Ciências Biológicas, Universidade Federal de Juiz de Fora, Juiz de Fora, Brazil; [3]Programa de Pós-Graduação em Zoologia, Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, São Paulo, Brazil; [4]Laboratório de Coleções Zoológicas, Instituto Butantan, São Paulo, Brazil; [5]Department of Sciences, Granada Sciences Park, Granada, Spain; [6]Grupo de Investigación en Animales Ponzoñosos y sus Venenos, Dirección de Producción, Instituto Nacional de Salud, Bogotá, Colombia; [7]Instituto de Investigación Biológica del Paraguay, Asunción, Paraguay; [8]Instituto de Biociências, Letras e Ciências Exatas, Universidade Estadual Paulista, São José do Rio Preto, Brazil; [9]Universidade Federal de Santa Maria, Santa Maria, Brazil; [10]Laboratório de Coleções Científicas, Universidade Católica de Brasília, Brasília, Brazil; [11]Coordenação de Zoologia, Museu Paraense Emílio Goeldi, Belém, Brazil; [12]Departamento de Botânica e Zoologia, Centro de Biociências, Universidade Federal do Rio Grande do Norte, Natal, Brazil; [13]Departamento de Engenharia e Meio Ambiente, Universidade Federal da Paraíba, Rio Tinto, Brazil; [14]Departamento de Ecologia e Zoologia, Centro de Ciências Biológicas, Universidade Federal de Santa Catarina, Florianópolis, Brazil; [15]Departamento de Zoologia, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais, Belo Horizonte, Brazil; [16]Facultad de Ciencias Naturales, Universidad Nacional de Tucumán, Tucumán, Argentina; [17]Centro de Ciências Biológicas, Universidade Federal de Pernambuco, Recife, Brazil; [18]Departamento de Biocências, Centro de Ciências Biológicas e da Saúde, Universidade Federal Rural do Semi-Árido, Mossoró, Brazil; [19]Departamento de Vertebrados, Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; [20]Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil; [21]Department of Zoology, Faculty of Sciences, Granada University, Granada, Spain; [22]Instituto de Biociências, Universidade Federal de Mato Grosso do Sul, Campo Grande, Brazil; [23]Instituto Federal de Educação, Ciência e Tecnologia de São Paulo, Avaré, Brazil; [24]Museo de Zoología, Escuela de Ciencias Biológicas, Pontificia Universidad Católica del Ecuador, Quito, Ecuador; [25]4 Potter Park, Cambridge, MA, USA; [26]Instituto Oswaldo Cruz, Fundação Oswaldo Cruz, Rio de Janeiro, Brazil and [27]Programa de Pós-Graduação em Ecologia e Evolução, Departamento de Ecologia, Campus Samambaia, Universidade Federal de Goiás, Goiânia, Brazil

Correspondence
Mario R. Moura
Email: mariormoura@gmail.com

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Abstract

1. Studying species interactions in nature often requires elaborated logistics and intense fieldwork. The difficulties in such task might hinder our ability to answer questions on how biotic interactions change with the environment. Fortunately, a workaround to this problem lies within scientific collections.
2. For some animals, the inspection of preserved specimens can reveal the scars of past antagonistic encounters, such as predation attempts. A common defensive behaviour that leaves scars on animals is autotomy, the loss of a body appendage to escape predation. By knowing the collection site of preserved specimens,

[Correction added on 03 November 2022 after first online publication, the affiliation of the author Gisele Winck has been revised]

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it is possible to assess the influence of organismal biology and the surrounding environment in the occurrence of autotomy.

3. We gathered data on tail loss for 8189 preserved specimens of 33 snake and 11 amphisbaenian species to investigate biological and environmental correlates of autotomy in reptiles. We applied generalized linear mixed effect models to evaluate whether body size, sex, life-stage, habitat use, activity pattern, biome, tropicality, temperature and precipitation affect the probability of tail loss in limbless reptiles.
4. We observed autotomy in 23.6% of examined specimens, with 18.7% of amphisbaenian and 33.4% of snake specimens showing tail loss. The probability of tail loss did not differ between snakes and amphisbaenians, but it was higher among large-sized specimens, particularly in adults and females. Chance of tail loss was higher for diurnal and arboreal species, and among specimens collected in warmer regions, but it was unaffected by biome, precipitation, and tropicality.
5. Autotomy in limbless reptiles was affected by size-dependent factors that interplay with ontogeny and sexual dimorphism, although size-independent effects of life-stage and sex also shaped behavioural responses to predators. The increase in probability of tail loss with verticality and diurnality suggests a risk-balance mechanism between species habitat use and activity pattern. Although autotomy is more likely in warmer regions, it seems unrelated to seasonal differences in snakes and amphisbaenians activity. Our findings reveal several processes related to predator–prey interactions involving limbless reptiles, demonstrating the importance of scientific collections to unveil ecological mechanisms at different spatio-temporal scales.

KEYWORDS
autotomy, biotic interaction, natural history, reptile ecology, scientific collection, tail loss

1 | INTRODUCTION

Understanding how biotic interactions are influenced by the environment is important to reveal the outcomes of the human driven disruption of the biosphere (Cardinale et al., 2012). However, studying species interactions in nature is often challenging because of the required fieldwork logistics and sampling effort (Torre Cerro & Holloway, 2021). Fortunately, a workaround to this problem lies within scientific collections. For some animal groups, examining preserved specimens can reveal evidence of past biotic interactions, such as nonlethal injuries as amputation and scars resulting from antagonistic encounters (Bateman & Fleming, 2009). Based on the collection site of preserved specimens, one can compare environmental conditions experienced by specimens with and without body scars (Guedes et al., 2020; Kuo & Irschick, 2016). Likewise, one can investigate the importance of biology, ecology, and biogeography on the occurrence of scars in preserved specimens (Costa et al., 2014; Fleming et al., 2007).

A plethora of antipredator mechanisms have evolved across different animal groups (Ruxton et al., 2019), but a well-known strategy to leave scars on animals' bodies is autotomy—the defensive behaviour of losing a body appendage (Emberts et al., 2019). This behaviour has evolved multiple times across the tree of life and plays an important role in predator–prey dynamics, competition, habitat selection, and many other ecological aspects (Bateman & Fleming, 2009; Fleming et al., 2007). Although preserved specimens can be used to identify environmental and biological correlates of autotomy, research on this topic should consider at least two points. First, some species can regenerate body parts after autotomy, which may hinder the discrimination between specimens that never used autotomy from those collected after regeneration and add uncertainty on how many times autotomy has been used by a given specimen. Second, the information extracted from preserved specimens must include potential autotomy correlates that vary across the geographical space and/or biological spectrum. Hence, limited spatial coverage will hardly capture environmental conditions potentially favouring autotomy, whereas the use of single or few related taxa can prevent the assessment of biological and ecological correlates varying above the species- or genus-level. Within this context, snakes and amphisbaenians (worm lizards) represent suitable taxa to

research autotomy since these animals do not regenerate lost body parts (Gans, 1978; Slowinski & Savage, 1995), and are widely distributed across the geographical and ecological space (Roll et al., 2017).

Snakes and amphisbaenians may shed their tails during antagonistic encounters (Costa et al., 2014; Guedes et al., 2020). Amphisbaenians can use this defensive behaviour only once (Gans, 1978), and although multiple tail breakage is possible in some snakes (Slowinski & Savage, 1995), it may not be very common (Costa et al., 2014; Dourado et al., 2013; Pleguezuelos et al., 2013). Because autotomy decreases the relative length of snake tail, the chances of new attacks hitting the remaining tail are likely lower compared to similar-sized individuals with relatively longer tail. The limited number—or absence— of autotomy repetitiveness in snakes and amphisbaenians, coupled with the lack of tail regeneration, make this defensive behaviour a unique and valuable antipredator strategy. Tail autotomy in squamates—including lizards—is often associated with greater predation intensity due to higher abundance and/or richness of predators (Cooper et al., 2004; Kuo & Irschick, 2016; Lin et al., 2017; Pianka, 1970; Vidal-García et al., 2011). Herein, we used thousands of preserved specimens of several snake and amphisbaenian species to investigate biological and environmental correlates of tail loss in extant limbless reptiles. We aimed to assess nine hypotheses regarding the correlates of tail loss in these taxa:

1. Body size: larger individuals have likely grown for more time, and therefore accumulated more chances of facing predation attempts relative to smaller ones (Halliday & Verrell, 1988). We expect a positive correlation between probability of tail loss and body size within each species.
2. Life stage: ontogenetic differences in morphology and behaviour may lead to different exposure rates to predators between life stages. For instance, juveniles may spend more time hidden (Gregory & Isaac, 2005) or be more lethally affected by predator attacks than adults (Willis et al., 1982), hampering the collection of juveniles with lost tails (Costa et al., 2014). Juveniles have been alive for a shorter period, which could also decrease chances of tail loss. We expect lower probability of tail loss in juveniles than in adults.
3. Sex: intraspecific differences in body size and behaviour may occur between male and female reptiles. In snakes, sexual size dimorphism (SSD) is often biased towards females whose larger size allows high reproductive output (Cox et al., 2007). The greater reproductive output of larger females can impose extended activity time or greater home range, and changes in dietary habits (Shine & Wall, 2006) that may ultimately increase the exposure of females to predators, at least among female-biased sexual dimorphic species. In addition, because male reproductive organs are found inside the tail base, male snakes may avoid tail autotomy to prevent decreasing mating success (Shine et al., 1999). Information on sexual differences in amphisbaenian body damage is virtually absent, which hampers more directional expectations regarding worm-lizards. For now, we expect the probability of autotomy to differ between sexes.
4. Activity time: snakes and amphisbaenians are most commonly preyed upon by squamate and bird species (Schalk & Cove, 2018). Since most birds and squamate reptiles have diurnal habits (Meiri, 2018; Wilman et al., 2014), we expect diurnal limbless reptiles to experience higher predation attempts and thus show higher probability of tail loss.
5. Habitat use: the exposure level of a species to predators can differ according to its habitat use. Fossorial species might be less exposed to aboveground predators relative to nonfossorial ones (Ferreira & Faria, 2021), whereas arboreal snakes may have more limited access to shelters and retreats relative to terrestrial species, increasing their susceptibility to predators. Indeed, a higher predation pressure on arboreal snakes is invoked to explain the greater diversity of defensive behaviours in arboreal than terrestrial species (Martins et al., 2008). We expect a higher probability of tail loss among species with higher levels of verticality in habitat usage.
6. Biome: at broad spatial scales, the biogeographic species pool of predators may differ across biomes. For instance, biomes with higher levels of vegetation complexity can support more predators (Monagan et al., 2017), which could make snakes and amphisbaenians more prone to predation attempts and increase autotomy frequency in those environments.
7. Tropicality: mammal, bird and reptile richness increase towards the equator (Moura et al., 2016; Roll et al., 2017). Since these vertebrates are the main predators of snakes and amphisbaenians (Schalk & Cove, 2018), predation intensity could be higher in the tropics due to greater predator diversity (Roslin et al., 2017). We expect chances of tail loss to be higher among specimens from tropical than temperate regions.
8. Temperature: squamate reptiles are ectothermic animals and their biology is highly dependent on external sources of temperature (Pianka & Vitt, 2003). Specimens from warmer localities can be more active than those from colder regions (Buckley et al., 2012) and increase their exposure time to predators. In contrast, the overheating risk may constrain the activity of tropical reptiles (Kearney et al., 2013; Sinervo et al., 2010), but it could still promote biotic interactions by increasing the potential for overlap between daily activities of prey and predators. Although the same reasoning could be applied to temperate reptiles facing shorter activity times, the lower predation pressure in high latitudes (Roslin et al., 2017) may counterbalance the outcome of high temporal niche overlap of species there. Hence, temperature may increase chances of encountering predators in multiple ways and increase the probability of tail autotomy.
9. Precipitation: high water availability might increase exposure of snakes and amphisbaenians for at least three reasons. First, heavier rainfalls may fill underground galleries more often and force fossorial species to the surface where aboveground predators are (Bates, 1993). Second, increased water availability affects invertebrate and amphibian abundance and activity, which may in turn increase prey availability to many amphisbaenians and snakes (Reynolds, 1982). Third, water helps reptiles to buffer heat

constraints along their climatic niche, with fully hydrated animals extending their activity time (Kearney et al., 2013). We expect higher chances of autotomy in limbless reptiles inhabiting wetter regions.

Without scientific collection, improving our ecological knowledge on species that are either 'hard-to-find' or recorded through fortuitous encounters, such as many snake and most amphisbaenian species (Colli et al., 2016), would be a very unreachable task. Our macroecological approach takes advantage in exploring potential patterns of tail loss across broad spatial and taxonomic scales.

2 | MATERIALS AND METHODS

2.1 | Data collection

We examined a total of 8847 preserved specimens of 58 snake and 22 amphisbaenian species, deposited in 61 collections from 11 countries (when not specified, acronyms follow Sabaj, 2020): Argentina: FML. Brazil: AAGARDA (Adrian A. Garda, field series, transferred to CHUFPB), CEPB, CHUFPB, CHUFPI, CHUFS, CHUFSC, CHUNB, CRIB (Coleção de Referência, Instituto Butantan), CZDP (Coleção Zoológica do Delta do Parnaíba), CZGB, FUNED, IBSP, IEPA, INPA, LZV, MBML, MCN, MCNR, MCP, MHNCI, MNRJ, MPEG, MTR (Miguel Trefaut Rodrigues, field series [to be transferred to MZUSP]), MZUESC, MZUFV, MZUSP, UFACF, UFC, UFG, UFMG-R, UFMT-R, UFPE, UFRGS, UFRN, ULBRA-TO (Centro Universitário Luterano de Palmas, Universidade Luterana do Brasil), URCA, ZUEC, ZUFMS, ZUFSM. Colombia: IAvH-R, ICN, MLS, MPUJ, UIS-R. Ecuador: MZUA, QCAZ. France: MNHN. Germany: ZSM. Paraguay: CZCEN, CZPLT, IIBP, MNHNP. Spain: DBAG. United Kingdom: NHMUK. Uruguay: MHMN, ZVC-R. United States of America: AMNH, CAS, FMNH, USNM.

For each specimen, we classified the condition of the tail tip: healed broken tail = 1, or intact tail = 0. Unhealed broken tail was treated as intact because we could not confirm whether breakage occurred before or after collection. We retrieved information on geographic coordinates of each collection site and kept in the database only species that had a minimum of 30 examined specimens, and at least five specimens with healed broken tail. We also obtained data on nine covariates: (a) body size (snout-vent length, in mm), (b) life-stage (binary, 0 = juvenile, 1 = adult), (c) sex (binary, 0 = male, 1 = female), (d) activity pattern (categorical; diurnal, cathemeral, nocturnal), (e) habitat use (categorical, four dummy variables: fossorial, aquatic, terrestrial, arboreal), (f) biome in which the specimen was collected (categorical; sensu Dinerstein et al., 2017), (g) tropicality, informing whether the specimen was collected in a tropical or temperate region (binary, 0 = temperate, 1 = tropical), (h) annual mean temperature (continuous, in °C), and (i) annual precipitation (continuous, in mm). Temperature and precipitation data were extracted from the collection site of each specimen based on the Worldclim database v. 2.1 (Fick & Hijmans, 2017), at the spatial resolution of 5 arc-min (*c*. 10 km). All variables were obtained at the specimen-level and refer to process occurring at the intraspecific-level, except for activity pattern and habitat use, which address processes occurring at the interspecific-level.

Whenever possible, life-stage and sex were determined through inspection of preserved specimens for sexually mature gonads and genital ducts or based on the minimum size of sexually mature male or female of each species. Life-stage was also inferred based on ontogenetic variation in species colour pattern for three species in our dataset. We did not find information on the minimum size of sexually mature specimens of seven species (*Amphisbaena bolivica*, *A. littoralis*, *Chironius bicarinatus*, *Ch. carinatus*, *Ch. gouveai*, *Ch. maculoventris*, *Echinanthera cephalostriata*), and therefore used the size thresholds available for their respective sister species. Details on the approach used to determine sex and life-stage for each species are available in Supporting Information (Table S1). We kept in our database only specimens whose combination of species (44 binomials), life-stage ('adult' vs. 'juvenile'), and sex ('female', 'male', or 'unknown' in a few cases) reached at least five specimens. Our final dataset included 8189 specimens of 33 snake (n = 6940 specimens) and 11 amphisbaenian (n = 1249) species (Figure 1), from six families (see Data Availability Statement).

2.2 | Standardization of predictor variables

To ease interpretation of predictor importance in subsequent analysis, we rescaled covariates in the range of 0 and 1. Sex was coded as a binary variable (0 = male, 1 = female), but 10% of specimens in our dataset (n = 843) were unsexed, including most or all specimens (n = 184) of four amphisbaenian species (*A. bolivica*, *A. kingii*, *A. littoralis*, *A. munoai*). To avoid discarding these unsexed species and to increase the statistical power of our analysis, we coded unsexed specimens as 0.5 (the midpoint between male and female code). The female proportion in our sample was 51.4% among all sexed specimens (51.7% in snakes and 49.8% in amphisbaenians). Analysis was repeated without unsexed specimens and returned qualitatively identical results (see Table S3).

We aggregated the binary variables of habitat use into a verticality metric (Oliveira & Scheffers, 2019), scored as: 0 = strictly fossorial, 0.25 = fossorial and terrestrial, 0.5 = terrestrial or aquatic, 0.75 = terrestrial and arboreal, and 1 = strictly arboreal. We also used species activity pattern to derive a diurnality metric, scored as 0 = nocturnal, 0.5 = cathemeral, 1 = diurnal. Since we could not find any information on the activity pattern of the worm-lizard *Cynisca leucura*, we assumed it to be cathemeral to avoid discarding all 49 specimens of this species.

All else being equal, large-sized specimens are often considered adults whereas the small-sized ones may represent juveniles. Thus, we could confound the potential effect of body size and life-stage on tail loss if the size-rescaling procedure had been applied to juvenile and adult specimens altogether. The same reasoning can be applied to sexual-size dimorphic species. Therefore, we rescaled body size between 0 and 1 separately for each combination of life-stage and

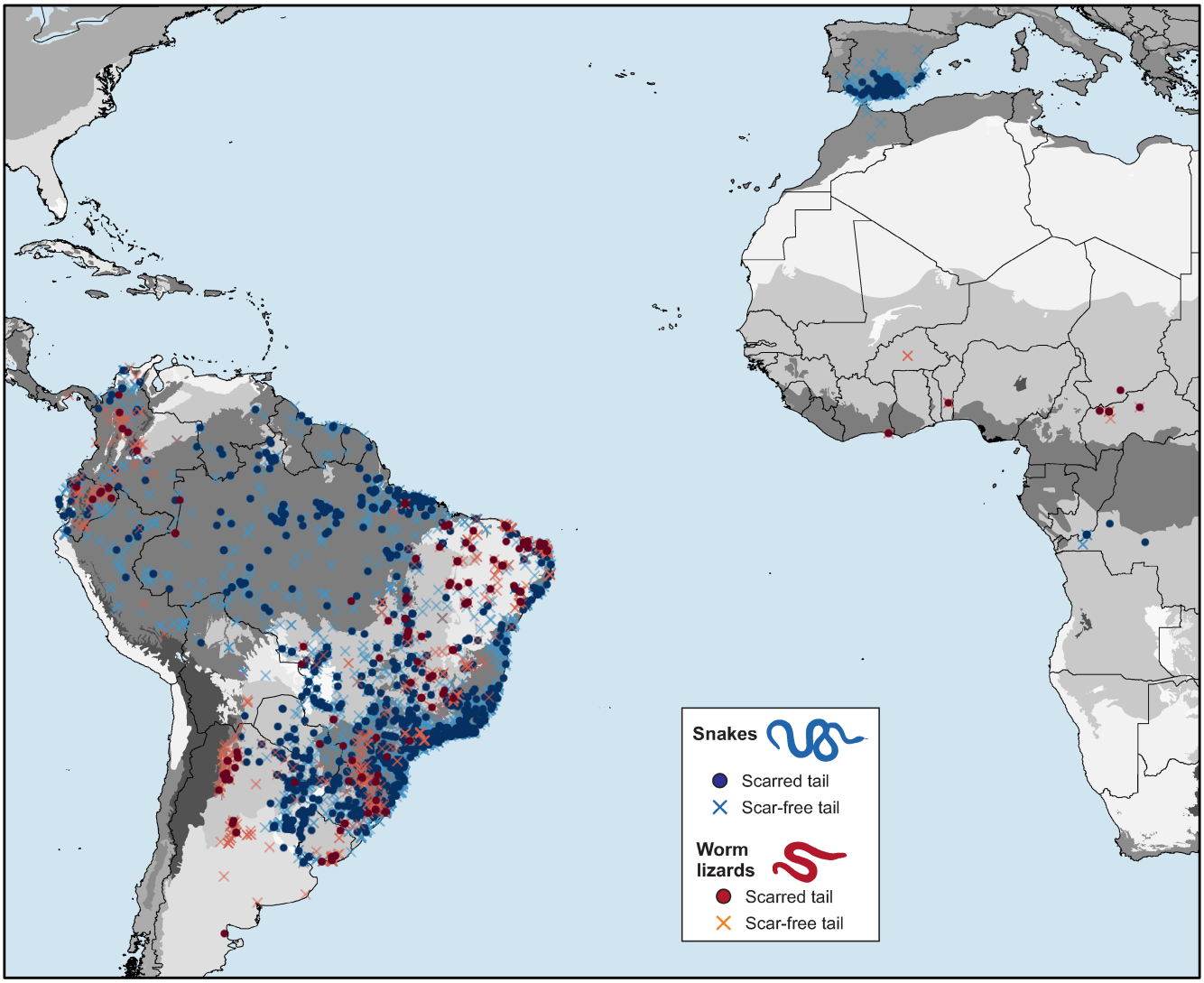

FIGURE 1 Geographical distribution of examined species of snakes and amphisbaenians. Symbol shape indicates the specimen tail condition, whereas symbol colours reflect the major taxonomic group. Grayscale colours in the background represent biomes (sensu Dinerstein et al., 2017).

sex (e.g., adult males, adult females, juvenile males, juvenile females) of each species. Unsexed specimens were pooled together as 'only adults' or 'only juveniles' before the rescaling procedure. While our rescaling procedure removed interspecific variation in body size, it also allowed the assessment of predictors with a strong interspecific size-dependent component. For instance, interspecific body size in reptiles tend to increase with verticality (Harrington et al., 2018) and diurnality (Meiri, 2010), which is also true for our data (Figure S1). Additional results with body size rescaled across all species are provided in Supporting Information (Table S3).

Finally, we rescaled temperature and precipitation in the range of 0 and 1 across all localities, regardless of the species. Both climatic variables were $\log_{10}$ transformed before the rescaling procedure to reduce skewness. We examined the multicollinearity of the predictors using the variance inflation factor—VIF (Kutner et al., 2004). As none of our predictors reached high levels of multicollinearity (VIF > 5), we kept all of them for the subsequent analysis.

2.3 | Statistical analyses

Our aim was to investigate how biological and environmental covariates affect the chance of tail loss in snakes and amphisbaenians. Although we were not interested in verifying the potential effects of species identity on the chance of tail loss, it was necessary to consider them in the analysis to control for pseudoreplication issues (Hurlbert, 1984). Due to the potential existence of dependence among specimens within a same species, we analysed our binary response variable (autotomy presence or absence) through a generalized linear mixed model (GLMM) with a binomial error distribution (Bolker et al., 2009). While it is possible to investigate the probability of tail loss through phylogenetic logistic regressions (Ives & Garland, 2010), limitations in our phylogenetic data (see below) led to model convergence issues that prevent application of this method. Hence, we fitted a GLMM to the data using only 'species' as random effect for intercept only. We did not include genus, family, or other

higher-level taxonomies as random effects to avoid mixed models overfitting, which could lead to singularity issues—that is, random effect variances estimated as zero (Bates et al., 2018; Matuschek et al., 2017).

We initially modelled the probability of tail loss as a function of the following fixed effects: (a) body size, (b) life-stage, (c) sex, (d) diurnality, (e) verticality, (f) biome, (g) tropicality, (h) temperature and (i) precipitation. We also included (j) taxonomic suborder (Serpentes vs. Amphisbaenia) as a fixed effect to evaluate potential differences in the probability of tail loss between snakes and amphisbaenians. We then applied a backward variable selection procedure based on the likelihood ratio test (LRT) to select only significant predictors. Briefly, we started the variable selection procedure by computing LRTs between the full model and all possible models with the removal of one predictor (Zuur et al., 2009). At each iteration, we registered the LRT value and the respective *p*-value associated with a simplified model (i.e., dropping one predictor), and removed the less significant predictor until all remaining covariates yielded $p \leq 0.05$. Computations were performed in R 4.1.0 using the *lme4* package (Bates et al., 2015).

Although the use of random effects in GLMM minimizes dependency issues among sampling units, the phylogenetic relatedness among species may produce positive phylogenetic autocorrelation in species traits (Freckleton, 2009), including the probability of tail loss. Also, the spatial proximity among collection sites may produce positive spatial autocorrelation in species distribution and ultimately affect trait spatial patterns (Kühn & Dormann, 2012). Therefore, we examined both the phylogenetic and spatial structure in the GLMM residuals of the final model through correlograms of Moran's *I* coefficients. This autocorrelation metric measures how similar (positive values) or dissimilar (negative values) sample pairs are, on average, based on their phylogenetic, temporal or spatial distance (Gittleman & Kot, 1990; Moran, 1950). Pair of samples can be divided in distance class intervals to depict the metric behaviour across increasing distances via correlogram plots. Herein, we used 14 distance classes for both the phylogenetic and spatial correlograms.

Building of a phylogenetic correlogram requires a phylogenetic tree to extract the pairwise phylogenetic distance between samples. For this purpose, we used a subset of 100 fully sampled global phylogenies for squamates (Tonini et al., 2016) trimmed to include only the 44 species in our dataset. The snake *Ch. gouveai* was missing in Tonini's tree and was treated as *Ch. bicarinatus*, which was its former name before the taxonomic split (Entiauspe-Neto et al., 2020). We added all specimens as polytomies at their respective species-level node and proceeded with computations of the phylogenetic correlogram for each tree, reporting the average results across the 100 trees. While our specimen-level phylogeny is necessary to verify phylogenetic autocorrelation in GLMM residuals, the presence of polytomies led to singularities in the phylogenetic covariance matrix, preventing the application of evolutionary model-based metrics of phylogenetic signal (e.g. Blomberg's *K* and Pagel's lambda). However, Moran's *I* is strongly correlated with evolutionary model-based metrics (Diniz-Filho et al., 2012), besides being particularly useful when model-based approaches are limited by the complexity of evolutionary processes (Hardy & Pavoine, 2012). All analyses were performed in R 4.1.0 using the *pgirmess* (Giraudoux, 2021), *phangorn* (Schliep et al., 2017) and *phylosignal* (Keck et al., 2016) packages.

3 | RESULTS

We analysed 8189 specimens of snakes and amphisbaenians of which 1934 showed healed broken tails (23.6% of total). The autotomy frequency was on average 33.4% among snake specimens and 18.7% across amphisbaenian specimens. Among snakes, we observed the lowest autotomy frequency in the Montpellier snake *Malpolon monspessulanus* (6.15%) and the highest autotomy frequency in the Gouvea's Sipo snake *Ch. gouveai* (75%). The amphisbaenians with the lowest and highest autotomy frequency were *A. heterozonata* (7.6%) and *Cy. leucura* (33.3%), respectively (Figures 2 and 3a). We did not find differences in probability of tail loss between snake and amphisbaenian specimens (LRT, $\chi^2 = 0.007$, $df = 1$, $p = 0.931$).

Tail loss frequency in snake specimens was 14.6% for juveniles and 29.5% for adults. Among amphisbaenians, 6.5% of juveniles and 19.3% of adults showed lost tail (Figure 3b). Overall, adult specimens of limbless reptiles showed 258.3% (range 203.9%–322.5%) more chances of having tail autotomy than juveniles (LRT, $\chi^2 = 263.172$, $df = 1$, $p < 0.001$, Table 1). Approximately 27.8% of female and 23.8% of male snakes had broken healed tails. For amphisbaenians, 16.5% of female and 19.3% of male specimens showed tail loss. The number of sexed specimens was almost 10-fold higher in snakes than in amphisbaenians, so we recommend caution in interpreting sex effects for amphisbaenians separately. Female specimens of limbless reptiles showed on average 37.3% (range 21.5%–55.1%) more chances of tail loss than males (LRT, $\chi^2 = 26.06$, $df = 1$, $p < 0.001$, Table 1). In addition, probability of tail loss was higher in large than small-sized specimens (LRT, $\chi^2 = 127.128$, $df = 1$, $p < 0.001$). For a same category of life-stage, sex and species, the largest specimen showed on average 275.3% (range 197.6%–373.5%) more chances of exhibiting tail loss relative to the smallest one (Table 1; Figure 4a).

The autotomy frequency varied among species with diurnal (22.6%), cathemeral (18.2%), and nocturnal (12.9%) activity pattern (Figure 3c), and the probability of tail loss increased with species' diurnality (LRT, $\chi^2 = 4.839$, $df = 1$, $p = 0.027$). Strictly diurnal species showed on average 116.4% (11.2%–321.1%) more chances of tail loss than those strictly nocturnal (Table 1). The autotomy frequency was smallest among species with fossorial habitat (15.8%), followed by those with aquatic (22.0%), terrestrial (32.4%) and arboreal habitat (36.0%, Figure 3d). Strictly arboreal species showed on average 204.8% (12.5%–726.2%) more chances of tail loss than those strictly fossorial (LRT, $\chi^2 = 4.536$, $df = 1$, $p = 0.033$, Table 1).

Temperature also influenced the probability of tail loss (LRT, $\chi^2 = 4.208$, $df = 1$, $p = 0.040$, Table 1; Figure 4b). Limbless reptile

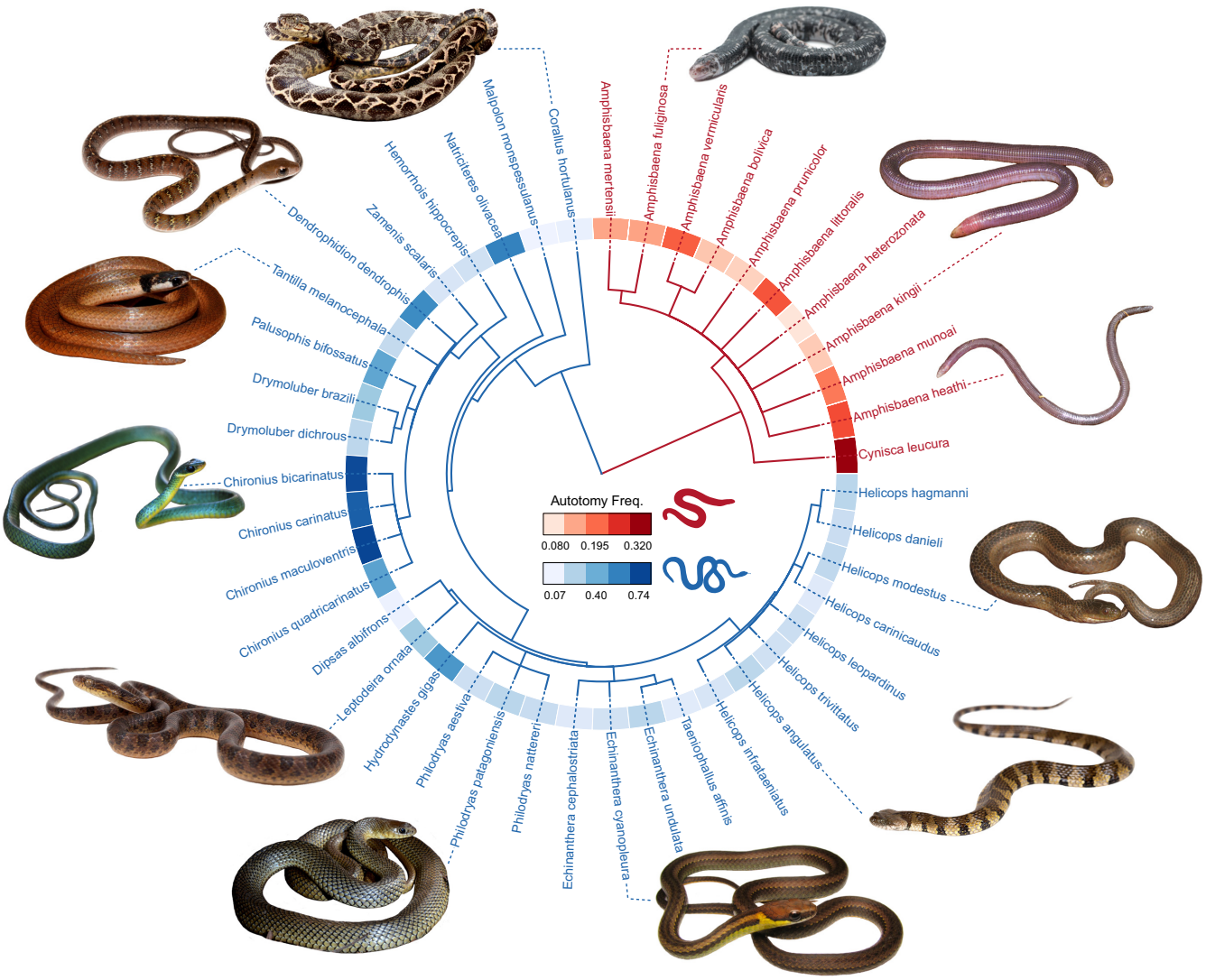

FIGURE 2 Autotomy frequency of snake and amphisbaenians species along the phylogeny. Photo credits: Diego J. Santana, Gustavo Pazmiño-Otamendi, Henrique C. Costa, Juan Carlos Sánchez, Juan David Fernández, Marcio Borges-Martins, Omar Torres Carvajal, Pedro H. Pinna, Raul Sales, Renato Gaiga, Santiago R. Ron, Weverton Azevedo.

specimens from the warmest locality in our study (annual mean temperature 29.5°C) showed on average 121.8% (3.8%–373.9%) more chances of tail loss than specimens from the coldest locality (3.5°C). We did not observe influence of precipitation (LRT, $\chi^2 = 0.013$, $df = 1$, $p = 0.908$), tropicality (LRT, $\chi^2 = 0.691$, $df = 1$, $p = 0.406$) and biome (LRT, $\chi^2 = 12.627$, $df = 8$, $p = 0.125$) on the chances of tail loss in limbless reptiles. The final model selected explained 22.5% of the variation in the data, with 14.7% of variation attributed to random effect (species identity) and 7.7% to fixed effects. Model residuals did not show spatial or phylogenetic structure (Figure S2).

4 | DISCUSSION

Autotomy represents an interesting and peculiar defensive behaviour widespread across the tree of life. Among reptiles, the tuatara and several squamate species are known to perform tail autotomy (Bateman & Fleming, 2009; Crnobrnja-Isailović et al., 2016; Guedes et al., 2020). But the knowledge on the factors affecting the probability of tail loss among reptiles is still scarce, mostly restricted to lizards (Bustard, 1968; Kuo & Irschick, 2016; Lin et al., 2017; Pafilis et al., 2009; Pianka, 1970; Smith, 1996), and usually based on single taxon approaches with restricted geographic scope. Based on a multitaxa framework and broad geographic coverage, we have demonstrated that while snakes showed higher autotomy frequency than amphisbaenians, there were no differences in the probability of tail loss between these taxa. The large unexplained variation in the probability of tail loss confirms the high complexity of autotomy ecology in limbless reptiles, but biological and environmental variables help explain tail breakage in these animals. For both groups combined, we found a higher probability of tail loss in adults than juveniles, females than males, and in large than small-sized specimens. Chances of losing the tail increased with verticality, diurnality,

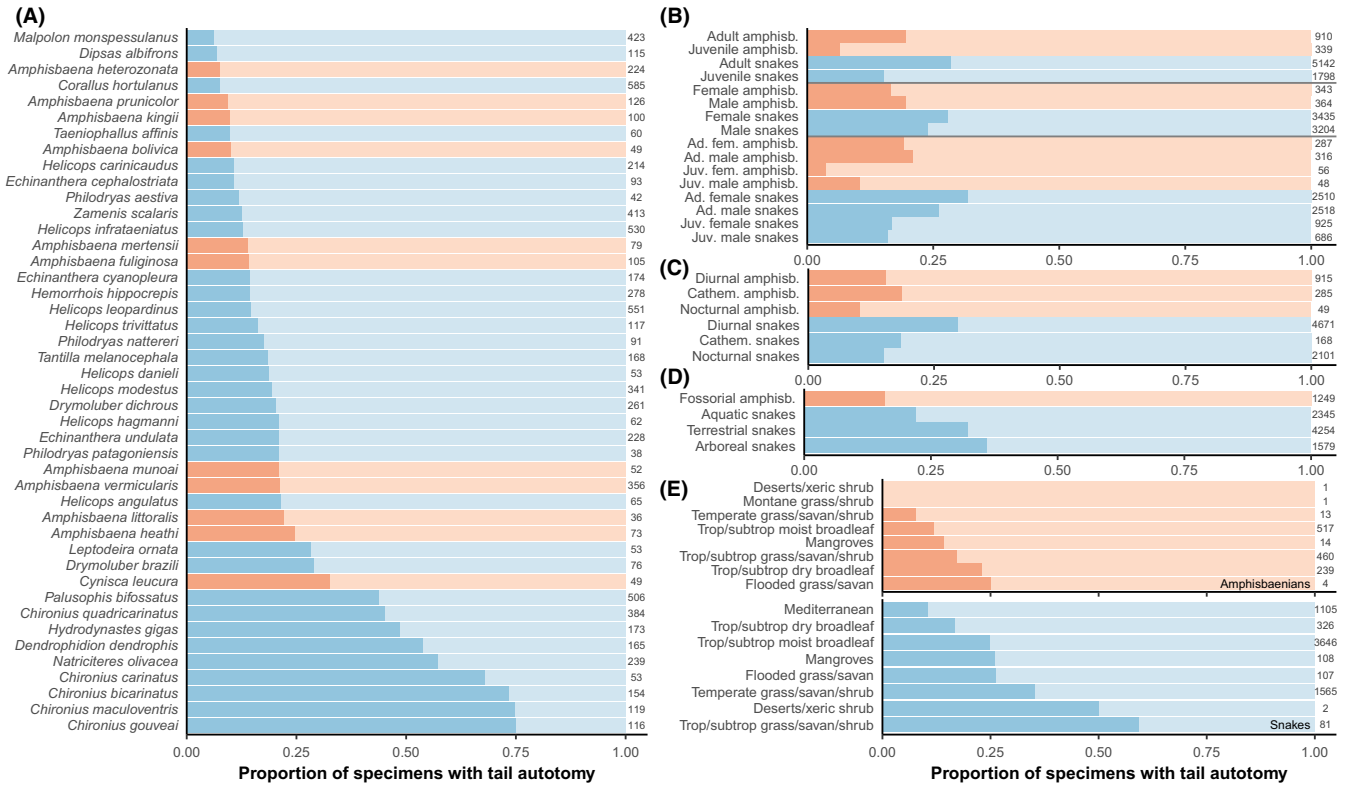

FIGURE 3 Proportion of snake and amphisbaenian specimens with autotomised tails. The frequency of tail loss is shown across (a) species, and categories of (b) life-stage and sex, (c) activity pattern, (d) habitat use and (e) biomes. The number of specimens in each category is shown on the right side of the panel. Bluish colours denote data on snakes and reddish colours refer to amphisbaenians.

TABLE 1 Generalized mixed effect model for the probability of tail loss among snake and amphisbaenian specimens. Likelihood ratio tests (LRT) were applied in a backward selection procedure starting with the full model. Predictor coefficients (Coef., lower CI and upper CI) are shown as odds ratio (instead of logit scale). Coefficient values >1 indicate the proportional increase in chances of tail loss (odds ratio) if the respective predictor value changes from 0 (min) to 1 (max), and the inverse occurs for coefficient values <1. Predictors are not significant if confidence intervals encompass the value of 1

Predictor	LRT	*p* Value	Coef.	Lower CI	Upper CI
Life-stage	263.172	<0.001	3.583	3.039	4.225
Body size	127.128	<0.001	3.753	2.976	4.735
Sex	26.060	<0.001	1.373	1.215	1.551
Verticality	4.536	0.033	3.048	1.125	8.262
Diurnality	4.839	0.029	2.164	1.112	4.211
Temperature	4.208	0.040	2.218	1.038	4.739

and temperature, but were unaffected by precipitation, tropicality and biome.

The increasing chance of tail loss in large-sized specimens is consistent with previous findings (Bateman & Fleming, 2009; Costa et al., 2014; Guedes et al., 2020). There are at least three nonmutually exclusive explanations for the size-dependence of autotomy. First, small-sized specimens can show high mobility and be more likely to scape antagonistic encounters before they are attacked (Downes, 2002). Second, small-sized specimens have a high surface-to-volume-ratio and can warm their bodies more quickly to a condition that allow fleeing with intact tails (Layne & Ford, 1984; Shine et al., 2000). This thermoregulatory benefit could operate synergistically with high mobility to improve escape capability and reduce chances of autotomy. Third, chances of encountering predators, and thus of losing the tail, accumulate through an individual lifetime, with large-sized individuals being relatively older (Halliday & Verrell, 1988). Within this context, specimens could have experienced autotomy in the past and grown (survived) to reach a larger size (Pike et al., 2008). Because neither the temporal aspect of autotomy nor the thermoregulatory constraints can be detected through preserved specimens, the mechanisms underlying size-dependence of autotomy remain an open question to ecological experiments.

After decoupling the influence of body size from life-stage, we still found lower chances of tail loss in juvenile than adult specimens. This size-independent variation in the probability of tail loss reinforces the role of ontogenetic behavioural differences in snakes and amphisbaenians. For instance, it may be possible that injury followed by death reduces autotomy frequency among juveniles (Willis et al., 1982). If collection of specimens in nature occurs at random regarding life-stage, one could expect to sample relatively more juveniles in species with low juvenile autotomy frequency, that is, more juveniles survive to be sampled. However, further inspection of our dataset did not indicate any relationship between juvenile proportion in the sample and autotomy frequency (Figure S3). Alternatively, juveniles can trade

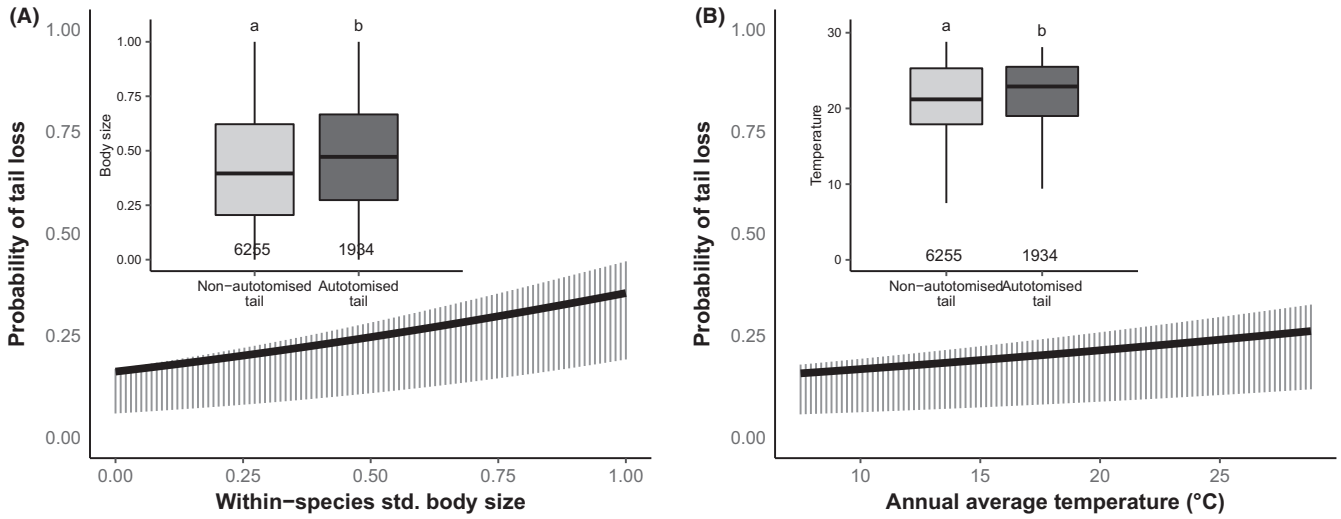

FIGURE 4 Predictors effect on the probability of tail loss in snakes and amphisbaenians. (a) Body size is normalized in the range of 0 and 1 separately for each species and life-stage. (b) Annual average temperature, values back transformed Celsius scale to facilitate interpretation. Internal boxplots show Kruskal–Wallis tests of differences in predictor median across specimens with and without tail autotomy.

activity time to bask and forage for safety (Webb & Whiting, 2005), and/or select suboptimal microhabitats to avoid predators (Webb et al., 2009), showing low propensity to tail autotomy in early lifespan. Juveniles may also use the tail for other purposes, such as luring behaviour to attract prey (Heatwole & Davison, 1976), or invest in different defensive behaviours rather than autotomy, such as dichromatism or mimicry (Costa et al., 2013), making them less likely to shed their tails during antagonistic encounters.

Female specimens showed higher chances of tail loss relative to males, particularly among snakes. All else being equal, the sex with greater relative tail length would have higher chances of having the tail attacked. The fact that relative tail length is male-biased in snakes and amphisbaenians (Santos, 2013; Shine et al., 1999), but autotomy frequency was female-biased in this study, reinforces the existence of a sex-related mechanism underlying this defensive behaviour. In our sample, more than half of snake species (and one amphisbaenian) showed female-biased SSD, whereas about one-tenth had male-biased SSD—the remaining species did not show significant SSD (Figure S4). Since chances of tail loss increase with body size, the sex effect on autotomy could result from female-biased SSD (e.g., Figure 5a,c). However, we bypassed this difficulty by rescaling body size within each sex and demonstrated the size-independent effect of sex on autotomy. One possible explanation is the reduced male survival to tail attacks due to hemipenis damage (Placyk & Burghardt, 2005). If so, species showing female-biased autotomy could also exhibit female-biased sex ratio as an indicative of reduced survival of autotomised males. Assuming that the female proportion in our sample represents the species sex-ratio found in nature, we did not observe relatively fewer males in snake and amphisbaenian species with female-biased autotomy, although there may be a trend in snakes (Figure 5b,d). Alternatively, males may show a low willingness to autotomise since an incomplete tail can reduced mating success (Shine & Shetty, 2001; Shine et al., 1999), or resource-driven behavioural differences can increase the exposure of a particular sex to predators (Lee et al., 2019), and ultimately raise autotomy frequency (Bateman & Fleming, 2011).

We confirmed our expectations about the influence of activity pattern and habitat use on the chances of tail autotomy, and also a potential risk-balancing mechanism between diurnality and verticality. On the one hand, most predators of snakes and amphisbaenians are diurnal squamates and visually oriented birds (Hansen et al., 2019; Meiri, 2018; Schalk & Cove, 2018; Wilman et al., 2014). On the other hand, arboreal species have limited access to shelters and are more exposed to predators than terrestrial or fossorial species (Ferreira & Faria, 2021; Martins et al., 2008). Therefore, by simultaneously showing arboreality and diurnality, snake species would face the worst of both worlds. The risk-balance between diurnality and verticality can be a mechanism to reduce predation pressure, which is supported by the fact that most arboreal snakes are nocturnal (Harrington et al., 2018). But if fossoriality and nocturnality allow species to reduce predation pressure, why is not such trait association more widespread among serpentiform squamates? One possibility is that fossoriality could increase interspecific competition for food resources. Competition is stronger among tropical snake assemblages, and in the absence of trophic partitioning, competitive exclusion can occur (Luiselli, 2006). Another reason for the rarity of fossorial nocturnal snakes may involve trade-offs among other niche dimensions (trophic, spatial, and temporal) and/or phylogenetic constraints limiting exploration of 'niche space', which has been revealed in lizards (Pelegrin et al., 2021). Improving data availability on activity pattern for snakes and amphisbaenians (Etard et al., 2020) should allow more thorough analyses on the adaptive value of different trait associations in serpentiform squamates.

Another interesting finding was the higher probability of tail loss in snakes and amphisbaenians from warmer regions. For instance,

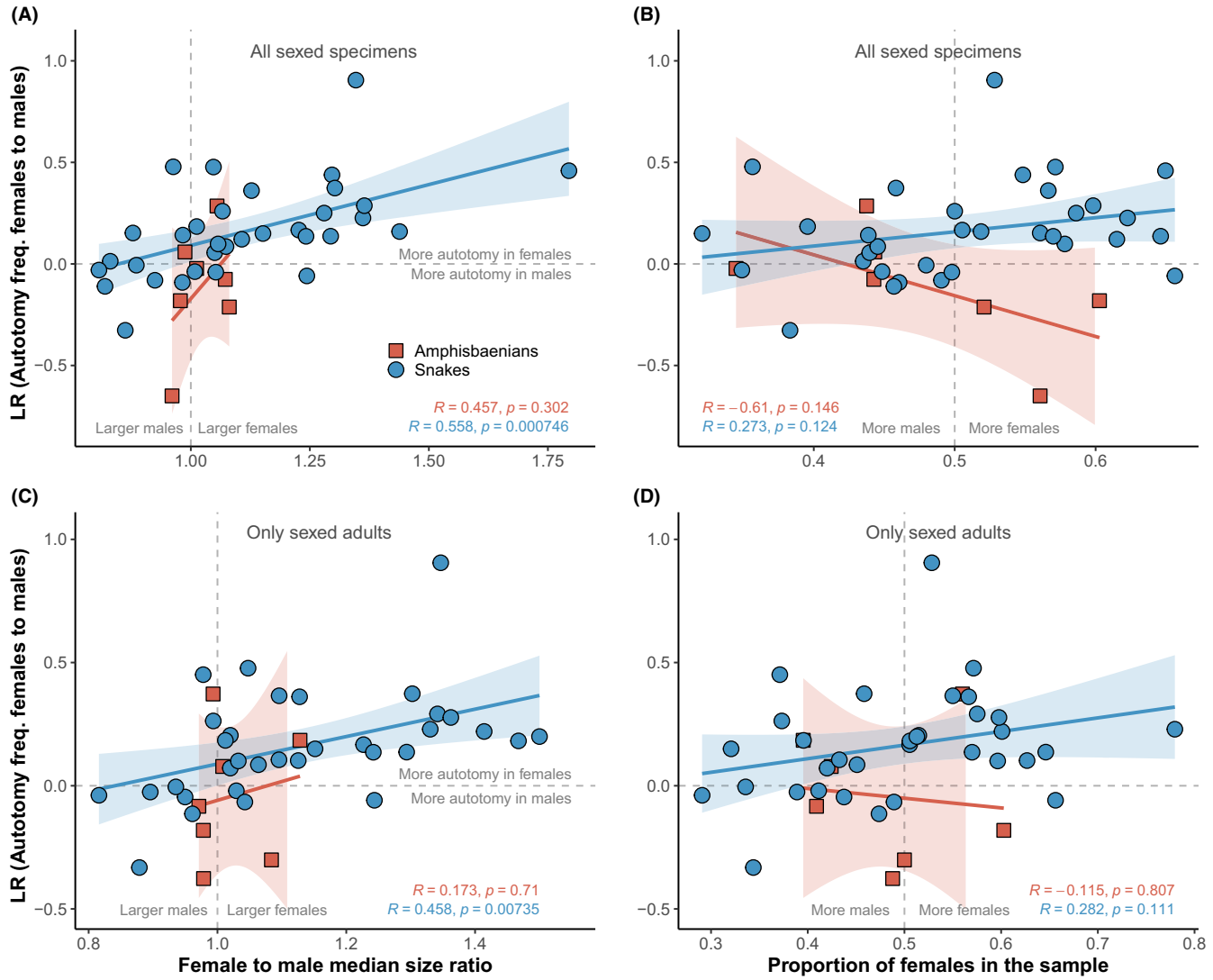

FIGURE 5 Relationship between autotomy frequency, sexual size dimorphism, and sample sex-ratio in snake and amphisbaenian species. Per species values were computed using (a, b) all available sexed specimens, or (c, d) only sexed adults. Log ratio (LR) of autotomy frequency of female to male >0 indicates more autotomy in females than males. *R* denotes the Pearson correlation coefficient.

movement and activity of snakes and amphisbaenians can either increase with temperature (Abe, 1984; Eskew & Todd, 2017; López et al., 2002), or specimens from warmer regions can support higher temperatures before seeking thermal refuges (Díaz-Ricaurte & Serrano, 2020), leading to longer activity time and higher chances of encountering predators. If so, autotomy events could be more common during warmer seasons. Although preserved specimens are useful to reveal seasonal activity patterns (Marques et al., 2001), it is not possible to assess seasonal variation in autotomy through preserved specimens since the tail loss event (if present) cannot be linked to the specimen collection date. Alternatively, the temperature can affect physiological processes that increase the ease of autotomy (Brattstrom, 1965; Daniels, 1984), although thermal effects on autotomy can also be bimodal (Bustard, 1968). Warmer regions can also have higher predation pressure, as already evidenced for lower latitudes and elevations (Roslin et al., 2017), which could impose risks not necessarily related to the amount of time a species remains active.

Although we have considered tail loss as a proxy for predation pressure, we acknowledge that at least two other interpretations are possible. First, elevated frequency of tail loss can imply an increase in intraspecific competition. Despite evidence supporting the role of competition for autotomy in some lizards (Itescu et al., 2017; Jaksić & Busack, 1984; Passos et al., 2013), there is virtually no confirmation for snakes or amphisbaenians. The observation of 'mating balls'—including tail wrestling—(Madsen & Shine, 1993; Shine et al., 2003) and other male–male combats in several snakes, but with no broken tails reported (Shine, 1978, 1994), suggest a somewhat limited contribution of intraspecific aggression driven autotomy, at least among snakes. Second, high autotomy frequency can result from low predatory efficiency, where eventually more prey could survive non-lethal attacks (Bateman & Fleming, 2011; Jaksić & Greene, 1984; Medel et al., 1988). Most available evidence in decoupling the roles of autotomy in squamates concerns insular lizards, where lower autotomy frequency was often attributed to efficient predators

such as raptors and small carnivores (Bateman & Fleming, 2011; Lin et al., 2017; Medel et al., 1988), and higher tail loss frequency was associated to less efficient predatory lizards and snakes (Itescu et al., 2017; Medel et al., 1988; Pafilis et al., 2009). For instance, autotomy frequency in snake populations shows a positive association with predator richness (Vidal-García et al., 2011). Considering that squamates are mainly preyed upon by other reptiles instead of avian and mammalian predators (Schalk & Cove, 2018), tail autotomy frequency may indeed reflect predation pressure, at least by specific kinds of predators.

Preserved specimens have been used to increase our knowledge on multiple aspects of species ecology, including diet and reproductive biology, malformation, and host–parasite interactions (Galbreath et al., 2019; Hilton et al., 2021; Johnson et al., 2003). Herein, we have shown how preserved specimens of snakes and amphisbaenians can be model organisms for research on autotomy and predation pressure. We highlight the role of size-independent effects of ontogeny and sex in shaping behavioural responses of limbless reptiles to potential predators, besides showing a potential risk-balance mechanism between the spatial (habitat use) and temporal (activity pattern) niche dimensions as a mechanism to reduce predation pressure. Our findings suggest that the temperature effect on autotomy is likely related to mechanisms such as the easiness of autotomy or increased predation in warmer regions. Additional research using preserved specimens with high resolution spatial and temporal data will allow the assessment of fine-scale determinants of biotic interactions, and ultimately uncover new pages of the tale on lost tails. We hope this research will shed light on the importance of museums and scientific collections as vital repositories of long-term biodiversity data (Meineke & Daru, 2021), which can be used to investigate a plethora of patterns and underlying mechanisms in many disciplines, including here research on biodiversity and global change.

AUTHOR CONTRIBUTIONS

Mario R. Moura, Jhonny J. M. Guedes, and Henrique C. Costa conceived the ideas. All authors contributed with data on examined specimens. Mario R. Moura designed methodology, analysed the data, and prepared the figures. Mario R. Moura and Jhonny J. M. Guedes led the writing. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST

Authors declare they have no conflict of interest.

DATA AVAILABILITY STATEMENT

The R-script and raw dataset supporting the results of this work are available at Dryad Digital Repository, https://doi.org/10.5061/dryad.83bk3j9v7 (Moura et al., 2022).

ORCID

Mario R. Moura https://orcid.org/0000-0002-7369-7502
Henrique C. Costa https://orcid.org/0000-0003-1663-2371
Teddy Angarita-Sierra https://orcid.org/0000-0002-5978-9312
Hugo Cabral https://orcid.org/0000-0002-0320-9411
Nathalie Citeli https://orcid.org/0000-0003-1587-9380
Frederico G. R. França https://orcid.org/0000-0001-6989-2455
Eliza M. X. Freire https://orcid.org/0000-0001-9486-6347
Paulo C. A. Garcia https://orcid.org/0000-0002-4789-7033
Ricardo Montero https://orcid.org/0000-0003-3314-5559
Daniel C. Passos https://orcid.org/0000-0002-4378-4496
Paulo Passos https://orcid.org/0000-0002-1775-0970
Juan M. Pleguezuelos https://orcid.org/0000-0003-2782-8281
Ana Lúcia C. Prudente https://orcid.org/0000-0002-4164-6815
Raul F. D. Sales https://orcid.org/0000-0001-6546-8956
Diego J. Santana https://orcid.org/0000-0002-8789-3061
Vinicius T. C. Silva https://orcid.org/0000-0001-8264-8764
Omar Torres-Carvajal https://orcid.org/0000-0003-0041-9250
Juan J. Torres-Ramírez https://orcid.org/0000-0002-3438-030X
Gisele R. Winck https://orcid.org/0000-0002-6876-4803
Jhonny J. M. Guedes https://orcid.org/0000-0003-0485-3994

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