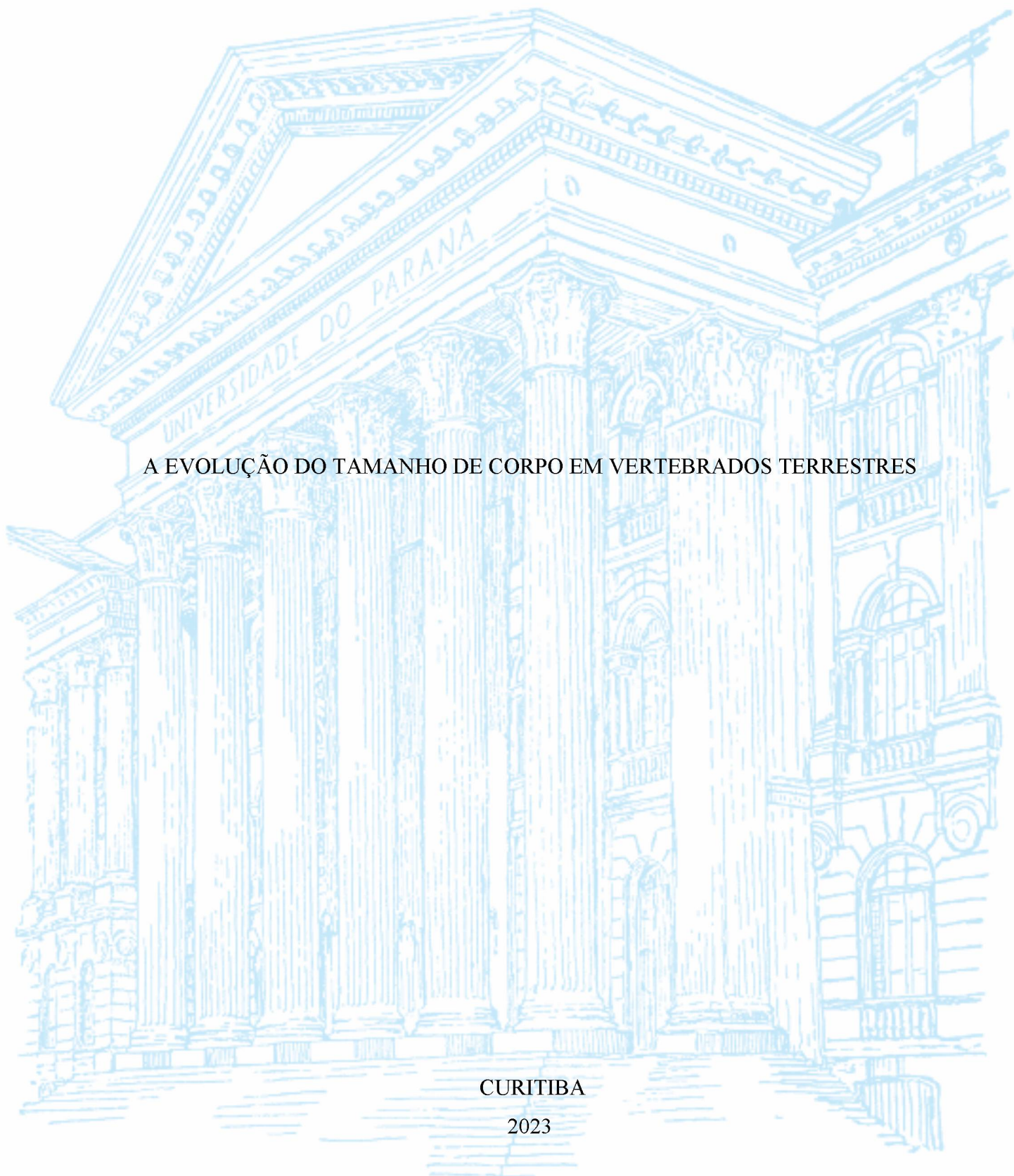UNIVERSIDADE FEDERAL DO PARANÁ

FERNANDA DE SOUZA CARON

A EVOLUÇÃO DO TAMANHO DE CORPO EM VERTEBRADOS TERRESTRES

CURITIBA

2023

FERNANDA DE SOUZA CARON

A EVOLUÇÃO DO TAMANHO DE CORPO EM VERTEBRADOS TERRESTRES

Dissertação apresentada como requisito parcial à obtenção do grau de Mestre em Ciências Biológicas - Zoologia, no Curso de Pós-Graduação em Zoologia, Setor de Ciências Biológicas, da Universidade Federal do Paraná.

Orientador: Prof. Dr. Marcio Roberto Pie

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TERMO DE APROVAÇÃO

Os membros da Banca Examinadora designada pelo Colegiado do Programa de Pós-Graduação ZOOLOGIA da Universidade Federal do Paraná foram convocados para realizar a arguição da dissertação de Mestrado de **FERNANDA DE SOUZA CARON** intitulada: **A EVOLUÇÃO DO TAMANHO DE CORPO EM VERTEBRADOS TERRESTRES**, sob orientação do Prof. Dr. MARCIO ROBERTO PIE, que após terem inquirido a aluna e realizada a avaliação do trabalho, são de parecer pela sua APROVAÇÃO no rito de defesa.

A outorga do título de mestra está sujeita à homologação pelo colegiado, ao atendimento de todas as indicações e correções solicitadas pela banca e ao pleno atendimento das demandas regimentais do Programa de Pós-Graduação.

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"Somehow, we'll find it. The balance between whom we wish to be and whom we need to be. But for now, we simply have to be satisfied with who we are."

— *Brandon Sanderson*

RESUMO

O tamanho corporal é uma característica fundamental em pesquisas evolutivas e ecológicas, pois está relacionada de forma alométrica com várias características importantes, como caracteres de história de vida e fisiológicos. No entanto, apesar de muitos estudos terem revelado padrões intrigantes sobre este caráter, ainda existem lacunas sobre as generalidades da evolução do tamanho corporal entre diferentes táxons de vertebrados terrestres. O principal objetivo dessa dissertação é explorar aspectos gerais e fundamentais sobre a evolução do tamanho de corpo em vertebrados terrestres. No capítulo I foram utilizados métodos filogenéticos comparativos recentes e grandes conjuntos de dados para explorar a evolução do tamanho corporal em vertebrados terrestres. Os resultados mostraram que, independentemente do táxon correspondente, a evolução do tamanho corporal difere dos modelos de taxa de evolução constante. Em todos os vertebrados terrestres, houve heterogeneidade significativa nas taxas de evolução dentro de cada grupo, uma relação positiva entre tamanho corporal e taxa de evolução, e taxas evolutivas mais rápidas próximas ao presente. Além disso, o mapeamento geográfico revelou algumas similaridades entre os táxons, mas nenhuma tendência latitudinal clara. Esses resultados sugerem que existem padrões gerais que governam a evolução do tamanho corporal em vertebrados terrestres, porém com algumas diferenças específicas para cada grupo. No capítulo II desta dissertação, o foco foi na evolução do dimorfismo sexual de tamanho (SSD – "*Sexual Size Dimorphism*") em aves, analisando como o caráter evolui e como está relacionado com o tamanho corporal. Apesar do SSD ter sido muito estudado ao longo dos anos, ainda restam dúvidas sobre se o grau de dimorfismo é capaz de afetar a taxa de evolução do tamanho de corpo ou mesmo se esses dois caracteres possuem covariância evolutiva. Deste modo, utilizamos um conjunto de dados de 4.761 espécies de aves para testar as previsões de quatro hipóteses: seleção sexual, fecundidade, divergência de nicho e alometria. Nossos resultados apontaram suporte para as hipóteses de seleção sexual, fecundidade e divergência de nicho, porém, esses resultados variaram entre as diferentes ordens de aves. Além disso, não encontramos evidências de que a direção do SSD afete a evolução do tamanho corporal, e também não identificamos uma relação clara entre o SSD e os fatores ambientais, como temperatura, precipitação e latitude. O que isto indica é que a evolução do dimorfismo sexual de tamanho em aves provavelmente é multifatorial, com a seleção sexual, fecundidade e divergência de nicho desempenhando papéis importantes em diferentes ordens de aves. Em conclusão, esta dissertação contribui para o entendimento dos padrões macroevolutivos do tamanho corporal em vertebrados terrestres e fornece novas informações sobre a evolução do dimorfismo sexual em aves. As análises realizadas nos permitem compreender melhor como essas características evoluíram ao longo do tempo e como são influenciadas por fatores ecológicos e espaciais.

Palavras-chave: alometria; macroecologia; métodos filogenéticos comparativos; movimento Browniano; partição de nicho.

ABSTRACT

Body size is a fundamental trait in evolutionary and ecological research, as it varies allometrically with several important characteristics, such as life history and physiological traits. However, despite many studies revealing intriguing patterns regarding this trait, there are still gaps in our understanding of the generalities of body size evolution among different terrestrial vertebrate taxa. In Chapter I of this dissertation, we used recent phylogenetic comparative methods and large datasets to explore body size evolution in terrestrial vertebrates, that is, amphibians, squamates, birds, and mammals. The results showed that, regardless of the corresponding taxon, body size evolution differs from constant-rate models. Across all terrestrial vertebrates, there was significant rate heterogeneity within each group, a positive relationship between body size and evolutionary rate, and faster evolutionary rates closer to the present. Additionally, the geographical mapping revealed some similarities among taxa, but no clear latitudinal trend. These findings suggest that there are general patterns governing body size evolution in terrestrial vertebrates but with some taxon-specific differences. In Chapter II of this dissertation, we focused on the evolution of sexual size dimorphism (SSD) in birds, analyzing how this trait evolves and its relationship with body size. Despite extensive research on SSD, uncertainties remain about whether the degree of dimorphism affects the evolutionary rate of body size or whether these two traits exhibit evolutionary covariance. Thus, we employed a dataset of 4,761 bird species to test predictions from four hypotheses: sexual selection, selection for fecundity in females, niche divergence between sexes, and allometry. Our results provided support for the hypotheses of sexual selection, fecundity, and niche divergence, although the support varied among different bird orders. Additionally, we found no evidence that the direction of SSD influences the evolution of body size, and we did not identify a clear relationship between SSD and environmental factors such as temperature, precipitation, and latitude. These findings indicate that the evolution of SSD in birds is likely multifactorial, with sexual selection, selection for fecundity, and niche divergence playing important roles in different bird orders. In conclusion, this dissertation contributes to our understanding of macroevolutionary patterns of body size in terrestrial vertebrates and provides new insights into the evolution of sexual dimorphism in birds. The analyses conducted allow us to better comprehend how these traits evolved over time and how they are influenced by ecological and spatial factors.

Keywords: allometry; Brownian motion; macroecology; niche partitioning; phylogenetic comparative methods; sexual selection.

SUMÁRIO

PRÓLOGO

Existem algumas características relacionadas ao organismo que são constantemente mais estudadas dentro da ecologia evolutiva, com um contínuo interesse na busca por padrões em diferentes contextos, como é o caso do nicho ecológico (PEARMAN et al., 2008; WIENS et al., 2010), do tamanho da distribuição geográfica da espécie (BROWN et al., 1996; ROSENZWEIG, 2010) e do tamanho de corpo dos indivíduos (BONNER, 2006; PETERS, 1983). Esse interesse se deve em parte às influências que essas características possuem sob outros caracteres e sob vários aspectos da evolução desses animais. Em particular, o tamanho do corpo de um ser vivo é uma ideia que atrai curiosidade há muito tempo, tendo sido uma questão de discussão para o próprio Darwin (1874). Esse caráter recebe destaque por sua extrema variação em magnitude, com seres vivos possuindo desde 10^{-13} g até 10^8 g (BROWN, 1995), assim como por sua variação alométrica com outros caracteres. Alometria pode ser observada quando o tamanho do corpo e outro caráter variam de acordo com diferentes taxas, como é o caso da taxa metabólica, do fluxo energético e de outras características da história de vida dos indivíduos (PETERS, 1983). Assim, incluindo o fato de ser de fácil mensuração, o tamanho do corpo é central em vários aspectos da ecologia evolutiva.

Devido às diferentes correlações do tamanho do corpo com outros aspectos dos organismos, os padrões conhecidos para esse caráter são diversos, mas existem alguns que são mais estudados. Dentre eles, estão a tendência de existirem mais espécies de tamanho pequeno do que grande, o que é refletido em uma distribuição de tamanho do corpo assimétrica positiva (HUTCHINSON; MACARTHUR, 1959). Porém ainda existem controvérsias sobre explicações para essas observações (ALLEN et al., 2006). Autores citam hipóteses relacionadas à energética dos organismos, filogenia, biogeografia, descontinuidade textural e interação de comunidades para essas explicações, mas um consenso ainda não é possível (ALLEN et al., 2006). Outros padrões encontrados e descritos são o aumento do tamanho do corpo com aumento da latitude (regra de Bergmann; BERGMANN, 1847), e o aumento do tamanho do corpo dentro de linhagens ao longo do tempo (regra de Cope; COPE, 1887). Todos esses padrões analisados ajudam a entender como o tamanho do corpo se comporta em diferentes grupos, mas existem lacunas sobre generalidades da evolução desse caráter entre táxons.

Além de padrões observados no tamanho de corpo entre espécies, existem variações notadas constantemente entre sexos de uma mesma espécie. O dimorfismo sexual de tamanho (SSD - "*Sexual Size Dimorphism*") é uma das características que frequentemente emerge da variação diferencial do tamanho do corpo entre indivíduos. Esse dimorfismo se apresenta

quando um dos sexos de determinada espécie possui tamanho maior do que o outro, sendo comum em animais e plantas que possuem papéis reprodutivos segregados (FAIRBAIRN, 2007). Geralmente, o SSD enviesado para os machos, ou seja, os machos maiores que as fêmeas, é mais comum entre vertebrados terrestres, enquanto que o SSD enviesado para fêmeas é mais comum entre invertebrados e vertebrados ectotérmicos, mas esse viés pode variar e divergir dentro desses grupos (FAIRBAIRN, 2007). Ainda não são bem definidas as causas para o surgimento do SSD e muitos grupos devem ter explicações particulares de suas histórias evolutivas para essa característica, mas geralmente se atribui grande parte dessa variação à seleção sexual (FAIRBAIRN, 2007). Apesar de consideráveis estudos sobre padrões e explicações para o SSD em diferentes táxons, pouco se sabe sobre como diferentes graus de SSD afetam a evolução de diferentes grupos.

Considerando que o SSD é a variação do tamanho do corpo em diferentes sexos, deve haver uma relação entre SSD e o tamanho do corpo da espécie em questão. A ideia de que o SSD aumenta com o tamanho do corpo quando o SSD é enviesado para machos, e que o SSD diminui com o tamanho do corpo quando é enviesado para fêmeas é chamada de regra de Rensch (RENSCH, 1950; 1959). Apesar desse padrão já ter sido observado para diversos grupos de animais (FAIRBAIRN et al., 2007), assim como evidências contrárias a essa regra (FAIRBAIRN et al., 2007), pouco é estudado sobre como a evolução do SSD afeta a evolução do tamanho do corpo. Por exemplo, ainda é desconhecido se altos graus de dimorfismo sexual de tamanho causam uma alta ou baixa taxa de evolução do tamanho do corpo, ou mesmo se esses dois caracteres possuem covariância evolutiva. Desse modo, entender como a evolução do SSD afeta o tamanho do corpo é importante para entender como diversas outras características da história de vida dos organismos são afetadas.

Nesse trabalho, foi analisado como ocorre a evolução do tamanho do corpo e do dimorfismo sexual em vertebrados terrestres. O capítulo I será dedicado para identificar padrões gerais na evolução do tamanho do corpo entre anfíbios, répteis, aves e mamíferos, focando em avaliar se a evolução segue um modelo onde a mudança é constante no tempo e se existem diferenças na evolução do tamanho do corpo entre os grupos. O capítulo II, por sua vez, será focado em como o SSD evolui em aves (considerando a maior disponibilidade de dados do grupo), analisando como acontece a evolução do caráter, como sua evolução e do tamanho do corpo estão relacionados e quais os correlatos espaciais e ecológicos para o surgimento do SSD. Assim, essa dissertação contribui para o entendimento de padrões macroevolutivos do tamanho do corpo em vertebrados terrestres.

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CAPÍTULO I

THE EVOLUTION OF BODY SIZE IN TERRESTRIAL VERTEBRATES

Capítulo em formato de artigo de acordo com as normas para submissão da revista *Ecology &*
Evolution, mas com as figuras inseridas no texto para facilitar a leitura.

1   **The evolution of body size in terrestrial vertebrates**

2

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10

11   **Abstract**

12   Body size is a fundamental trait in evolutionary and ecological research, given that it varies

13   allometrically with several relevant features, such as life-history and physiological traits.

14   Although previous studies uncovered many intriguing patterns, finding general principles of

15   body size evolution in vertebrates has been elusive. In this study, we take advantage of recent

16   advances in phylogenetic comparative methods and the availability of large-scale datasets to

17   explore body size evolution in terrestrial vertebrates. Ancestral character reconstruction and

18   disparity-through-time plots showed considerable variation in body size evolution, both across

19   lineages and over time. In addition, regardless of the corresponding taxon, posterior predictive

20   simulation demonstrated several consistent ways in which body size evolution in those groups

21   departed from constant-rate models, namely: (1) there was considerable rate heterogeneity

22   within each taxon, (2) there was a positive relationship between body size and its rate of

23   evolution (i.e., large-bodied animals evolved faster than small-bodied ones), and (3) faster

24   evolutionary rates near the present. Finally, geographical mapping of body mass and

25   evolutionary rates revealed some similarities across taxa, but no clear latitudinal trends. Overall,

26   these results indicate that there may be general patterns that govern body size evolution on large

27   scales in terrestrial vertebrates, with some intriguing taxon-specific differences.

28   **Keywords**: macroevolution, body size, phylogenetic comparative methods, model adequacy,

29   posterior predictive simulation.

30

1. Introduction

Understanding the causes and consequences of body size evolution has been at the core of ecological and evolutionary research since the beginning of those fields (Bonner, 2006). In part, this interest stems from the ease of measuring body size and its association with several allometrically-related traits (Peters, 1983). As a consequence, body size can be used as a proxy for other traits that are difficult to measure, such as metabolic rate, ingestion rate, and mass flow (Peters, 1983). Given this importance, several studies have sought to identify patterns of body size variation, which helped to elucidate many aspects related to the ecology and evolution of organisms (Brown, 1995; Peters, 1983). For instance, a prevalent observation in a variety of animal groups is that there are many more small-bodied species than large-bodied ones (Hutchinson & MacArthur, 1959). Indeed, previous studies found that a right-skewed distribution of body size is frequent across many groups of organisms (Brown, 1995). Another prominent debate has been on the positive relationship between latitude and body size, known as Bergmann's rule (Bergmann, 1847). Although no single mechanism has been proposed to explain this observation (e.g., heat-conservation hypothesis [Olalla-Tarraga et al., 2006]; starvation resistance hypothesis [Cushman et al., 1993]; phylogenetic constraints [Queiroz & Ashton, 2004]), Bergmann's rule has received mixed support in the literature (Ashton & Feldman, 2003; Henry et al., 2023; Pincheira-Donoso et al., 2008). Another recurring pattern in empirical data is the island rule (Benítez-López et al., 2021; Lomolino, 2005; Lomolino et al., 2013), which describes the tendency of small animals to evolve into larger sizes on small islands, while large animals tend to evolve into smaller sizes on the same islands, possibly due to reduced predation, competition, or due to resource limitation (Lomolino et al., 2013). Finally, Hutchinson (1959) proposed a link between body size and competition within communities, hypothesizing that two species at the same trophic level can coexist only if their size ratio was sufficiently large to avoid competitive exclusion. Even though these patterns have been

56 commonly explored, we still lack a comprehensive understanding of the evolution of body size,

57 particularly with respect to the possibility of general principles that apply across different taxa.

58 The advent of phylogenetic comparative methods spurred new efforts into modeling

59 changes in body size at a macroevolutionary scale. In particular, evolutionary studies, for the

60 most part, have focused on assessing the relative fit of different models of evolution, with

61 inconsistent results depending on the particular taxon. For instance, studies on mammals have

62 found evidence that body size evolves according to an early burst model, in which much of the

63 evolution in body size takes place at the beginning of the clade, and the evolutionary rate would

64 decrease over time, consistent with the idea of radiation into empty niches (Cooper & Purvis,

65 2010). However, Harmon et al. (2010a) found no evidence for this claim when they examined

66 a variety of animal clades, concluding that models of random walk and selective peak were

67 better supported. Likewise, Venditti et al. (2011) suggest a more complex model in which

68 clades within mammals evolve according to separate rates of evolution, and not according to a

69 single overall rate, whereas Landis & Schraiber (2017) incorporated pulses of evolutionary

70 change through time in a novel approach and got more support from this model than from an

71 early burst or Brownian motion. Therefore, the number of models proposed to explain body

72 size evolution is large, yet there is still no consensus about which one best describes empirical

73 data. A caveat commonly missed in these studies is that the model fit is usually evaluated among

74 a limited set of models (Cooper & Purvis, 2010; Harmon et al., 2010b; Landis & Schraiber,

75 2017). As a result, the best-fit model may still show a poor fit to the data but is still the best

76 choice given the alternative models proposed (Pennell et al., 2015). However, to the best of our

77 knowledge, no study to date tested the adequacy of models in body size evolution among

78 terrestrial vertebrates, an essential approach to determine whether they are good descriptors of

79 their evolution.

80   Despite the lack of a consensus regarding the best model for representing body size

81   evolution in previous studies, there are overarching patterns concerning the variation of

82   evolution across character states and lineages. For instance, Cooper & Purvis (2009) showed

83   that large-bodied mammals have faster rates of evolution, although some but not all clades

84   showed a high evolutionary rate for small sizes as well. Similarly, Baker et al., (2015) found

85   evidence that large-bodied ancestors tend to generate changes in the size of their descendants

86   with higher magnitude than when the ancestor is small. These differences in large-bodied

87   species might be explained by the relaxation of size-linked constraints, such as genetic or

88   developmental, or by the low population densities characteristic of larger species (Stanley,

89   1979), but none of these explanations were consistently supported in previous studies (Baker et

90   al., 2015; Cooper & Purvis, 2009). Furthermore, given the physiological differences in

91   ectotherms and endotherms, the rate of body size evolution could also be expected to vary

92   among different taxa. Considering that endotherms have higher metabolic rates than

93   ectotherms, the minimum body size in endotherms is constrained by the energetic demands of

94   generating heat, as the relative metabolic rate increases with decreasing size (Peters, 1983).

95   Additionally, ectotherms might have a constraint in the maximum body size by a minimum

96   mass-specific metabolic rate, which decreases with increasing size but in ectotherms also

97   increases with increasing temperature (Makarieva et al., 2005). Therefore, ectotherms in

98   warmer areas could have larger body sizes than similar species in colder areas (Makarieva et

99   al., 2005). These and other physiological differences might affect their respective body size

100   distributions and consequently affect how these sizes evolve. Regardless, all of these studies

101   usually focus on understanding the dynamics of a single class of animals, such as mammals

102   (Baker et al., 2015; Cooper & Purvis, 2010; Venditti et al., 2011), birds (Cooney et al., 2017),

103   or fishes (Albert & Johnson, 2012), but comparisons across taxa are scarce (e.g., Harmon et al.,

104   2010; Landis & Schraiber, 2017). These comparisons might reveal general patterns of body size

105   evolution that might not be linked to physiological or ecological differences across taxa.

106   In this study, we provide a comprehensive exploration of patterns of body size evolution

107   across terrestrial vertebrates, focusing particularly on amphibians, squamates, birds, and

108   mammals. We begin by using phylogenetic comparative methods to assess how body size

109   evolution evolved over time and across terrestrial vertebrate lineages. Then, we use posterior

110   predictive modeling to test for different ways in which body size evolution departs from a

111   constant-rate model of evolution. Finally, we contrast geographical patterns in rates of body

112   size evolution. Hence, using this approach, we expected to find (1) heterogeneity across

113   lineages and through time in the evolutionary rate of body size in terrestrial vertebrates; (2) that

114   body size evolution increases as species become larger in all terrestrial vertebrates, given the

115   relaxation of size-linked constraints; (3) a positive relationship between the average sizes of a

116   geographical region and its average rate of body size evolution, given the previous prediction;

117   and (4) that ectotherms and endotherms differ in their rates of evolution.

118

119   **2.   Materials and Methods**

120   *2.1.   Data sources*

121   We obtained data on the phylogenetic relationships of amphibians, squamates, birds,

122   and mammals from Jetz and Pyron (2018), Tonini et al. (2016), Jetz et al. (2012), and Upham

123   et al. (2019), respectively. For each taxon, we compiled body mass data from several sources.

124   Whenever there were differences among these sources, we calculated the mean, the median,

125   and the maximum body size across them to account for this variability and repeated separate

126   analyses with each alternative dataset to ensure the robustness of our results. For amphibians,

127   we obtained body mass (g) data from Oliveira et al. (2017; N=552 species). We repeated

128   analyses using snout-vent length (SVL) (mm) as a measure of body size, also obtained from

129   Oliveira et al. (2017), given that more data exists on SVL for amphibians (N=5,030). For

130   squamates, body mass (g) data were obtained for a total of 9,709 species from Feldman et al.

131   (2016; N=9,699), Meiri (2019; N=1,991), and Myhrvold et al. (2015; N=2,255). Given that

132   SVL (mm) is a common measure of body size in squamates, we also compiled it for 9,703

133   squamate species from Feldman et al. (2016; N=9,699), Myhrvold et al. (2015; N=1,509), and

134   Meiri (2018; N=5,934). We obtained body mass (g) data for birds from Wilman et al. (2014;

135   N=5,265), Lislevand et al. (2007; N=532), Ocampo et al. (2021; N=1,132), and Myhrvold et al.

136   (2015; N=7,901), for a total of 9,093 avian species. Finally, we obtained body mass (g) for

137   mammals from Wilman et al. (2014; N=4,986), Ocampo et al. (2021; N=227), Faurby et al.

138   (2020; N=5,422), and Jones et al. (2009; N=3,019), for a total of 5,548 mammal species with

139   at least one measure of body mass. Spatial data were retrieved from IUCN (2022) for

140   amphibians, squamates, and mammals and from BirdLife International (2021) for birds.

141

142   *2.2.   Analyses*

143   We began our analyses by exploring variations in body size over evolutionary time and

144   across lineages. First, we visualized interspecific variation in body size for amphibians,

145   squamates, birds, and mammals using histograms of log-transformed data, both for the entire

146   group as well as for selected subclades. Given that results using mean, median, and maximum

147   estimates for each species were nearly identical (Figures 1; Appendix A: Figures A1-A4), we

148   only considered analyses using species means in later tests. We mapped body size evolution

149   onto each phylogeny (using only one representative topology) using the contMap function in

150   "phytools" 0.7–70 (Revell, 2012), which uses maximum likelihood to estimate ancestral states.

151   We also generated disparity-through-time (DTT) plots of body size using the dtt function in

152   "geiger" 2.0.7 (Pennell et al., 2014a) to assess how the average disparity in each clade changed

153   over time. To account for phylogenetic uncertainty, we repeated DTT calculations for 100

154   alternative topologies for each taxon. We compared the observed results with simulated data,

155   computed as the average between 100 simulations for each of the alternative topologies

156   indicated above, to assess if there were periods in which body size evolution was faster or

157   slower than expected based on a constant-rates model. All body size measures were log10-

158   transformed prior to the analyses.

159   We used posterior predictive simulations to explore ways in which body size evolution

160   could depart from a constant-rate model. We began by fitting a Brownian Motion (BM) model

161   to empirical body size data using fitContinuous in "geiger" 2.0.7 (Pennell et al., 2014a). Under

162   this model, the covariance of species traits is directly proportional to their shared evolutionary

163   history. Then, we assessed the adequacy of this model using "arbutus" 0.1 (Pennell et al.,

164   2014b). This approach involves three main steps: (1) it calculates several test statistics of the

165   data according to the chosen model of evolution, (2) it simulates datasets (N=1 in this study for

166   each alternative topology, see below) on the phylogeny using the parameters of the model

167   estimated from the empirical data, and (3) the observed test statistics are compared to the

168   simulations. These test statistics inform if and how the empirical data deviates from datasets

169   simulated under the model in question. Here, we used four test statistics: M_{sig}, the mean of the

170   squared contrasts, which indicates if the overall rate of evolution might be under or

171   overestimated; C_{var}, the coefficient of variation of the absolute value of the contrasts, used to

172   assess the extent of heterogeneity in the rate of evolution across the phylogeny; S_{asr}, the slope

173   of a linear model fitted to the absolute value of the contrasts against the ancestral state inferred

174   at the corresponding node, showing variation in the rate of evolution relative to the trait state;

175   and S_{hgt}, the slope of a linear model fitted to the absolute value of the contrasts against node

176   depth, which can detect variation in the rate of evolution in time, identifying early bursts of

177   evolution. More details about the test statistics can be obtained from Pennell et al. (2015). We

178   repeated this process for 1000 alternative topologies available for each taxon to account for

179   phylogenetic uncertainty. All analyses were carried out in R 4.1.1 (R Core Team, 2023).

180   Finally, we assessed whether there is a spatial relationship between the average species

181   mass of a region and its body size evolutionary rate. To achieve this, we mapped globally the

182   median body size of the species present in each cell, as well as their median evolutionary rate.

183   TreeAnnotator v2.6 (Bouckaert et al., 2019) was used to create maximum clade credibility trees,

184   given that it is computationally challenging to calculate tip rates using a distribution of trees

185   with thousands of tips. Then we calculated the rate of evolution of body size (mass and SVL)

186   of each species using "RRphylo" 2.7-0 (Castiglione et al., 2018). This method is based on

187   phylogenetic ridge regression and assigns a different rate to each branch of the tree without

188   applying an evolutionary model a priori (Castiglione et al., 2018). The maps were made using

189   a projection of 10-arc minutes, using the packages "rgdal" 1.6-5 (Bivand et al., 2023), "sf" 1.0-

190   12 (Pebesma, 2018), and "raster" 3.6.20 (Hijmans et al., 2023) in R 4.1.1 (R Core Team, 2023)

191   and QGIS (QGIS Team, 2023) to process the geographical data.

192

193   **3.   Results**

194   There was considerable variation within and between taxa in their body mass

195   distribution, both in terms of their means and degree of skewness (Figure 1). The distribution

196   of body mass in birds and mammals is particularly skewed, whereas amphibians show a notably

197   lower level of skewness (Figure 1E). Moreover, birds and mammals show larger body mass

198   compared to amphibians and squamates, with mammals having the largest mass and amphibians

199   the smallest (Figure 1E). When examining groups within classes, both of the studied amphibian

200   orders are approximately symmetric in their distributions, with a few caudate species showing

201   unusually large body mass (Figure 1A). In squamates, Serpentes show the largest mean body

202   mass with an almost symmetrical distribution, whereas the other groups present a longer right

203   tail and lower means (Figure 1B). Within Aves, Apodiformes and Passeriformes have the

204   smallest body masses in the class, with longer right tails than the other groups (Figure 1C).

205   Finally, in mammals, Chiroptera and Eulipotyphla exhibit the smallest body mass, followed by

206   Rodentia, whereas Carnivora, Cetartiodactyla, and Primates have a larger mass, with the first

207   two also having longer right tails (Figure 1D). SVL analyses uncovered a similar trend in

208   amphibians and squamates, but with longer right tails in both distributions, especially in

209   squamates, given that the longer length of Serpentes causes the distribution to be almost

210   bimodal (Appendix A: Figure A3). It is important to note that we did not include all the orders

211   of birds and mammals in the figures, choosing only those with the highest species richness to

212   facilitate visualization and comparison.

213
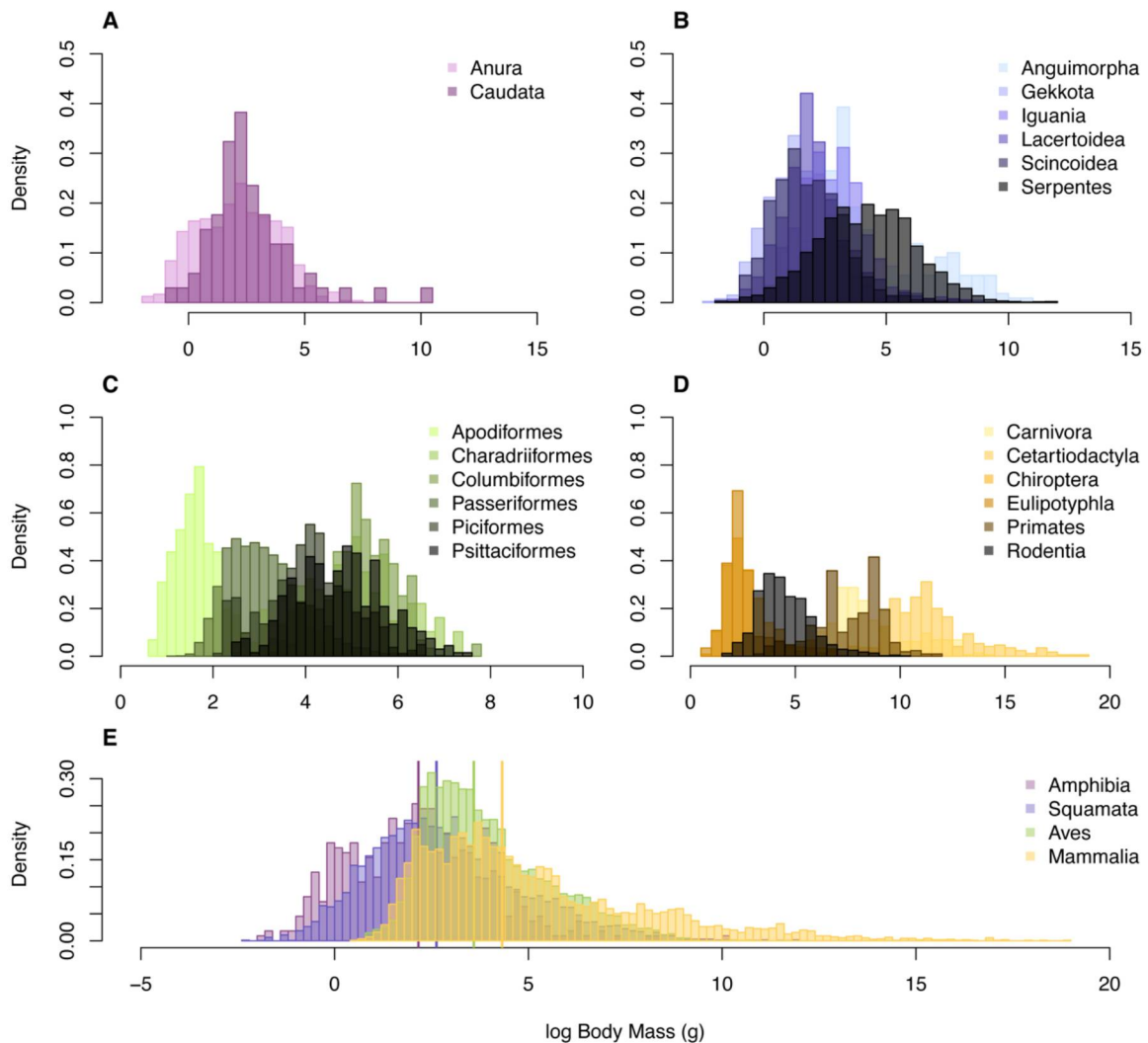
Figure 1. Density distribution of body mass (g) in terrestrial vertebrates. Distributions are shown for amphibians (A), squamates (B), birds (C), and mammals (D) separated by selected subclades, and for the entire taxa (E). Lines in (E) indicate the median body mass for each lineage. Body mass estimates for squamates, birds, and mammals were averaged across sources.

Mapping body mass evolution onto the corresponding phylogenies indicated highly complex evolutionary patterns, with some intriguing similarities (Figure 2). Small and intermediate body masses in general tend to be widely distributed across the history of each group, whereas larger species seem to be concentrated in relatively small, terminal branches (Figure 2). The largest body mass in amphibians appears to be equally distributed between

225   Anura, Caudata, and Gymnophiona (Figure 2A), but the reduced number of amphibian species

226   with body mass information (N=552) relative to the total number of amphibians in the

227   phylogeny (N=7,238) may bias this pattern. In squamates, the largest body masses are

228   concentrated mainly in the branches closely related to Serpentes, whereas other lineages

229   remained with smaller average masses, with a few branches evolving increased body size, such

230   as Anguimorpha and Iguania (Figure 2B). Birds seem to have evolved from relatively larger

231   body masses, which became smaller mainly in Passeriformes and Apodiformes. On the other

232   hand, Charadriiformes, Columbiformes, Piciformes, and Psittaciformes largely tended to retain

233   their ancestral condition (Figure 2C). Mammals showed a similar overall trend in relation to

234   birds, but some lineages have attained even larger masses in more recent times. Indeed,

235   Cetartiodactyla, Carnivora, and Primates have lineages with the largest body masses of all

236   terrestrial vertebrates (Figure 2D). Chiroptera and Eulipotyphla exhibited a decrease in average

237   body mass compared to the mammalian ancestor, which in turn is similar in mass to the average

238   size of Rodentia. Analyses using SVL showed a notable difference, with the amphibian ancestor

239   estimated with a much larger length, which is maintained in Gymnophiona and Caudata, the

240   lineages with the largest lengths in amphibians (Appendix A: Figure A5A), whereas Anura

241   evolved towards smaller lengths. In squamates, Serpentes remain the group with the largest

242   lengths, but the vast majority of lineages have evolved species with greater lengths (Appendix

243   A: Figure A5B).

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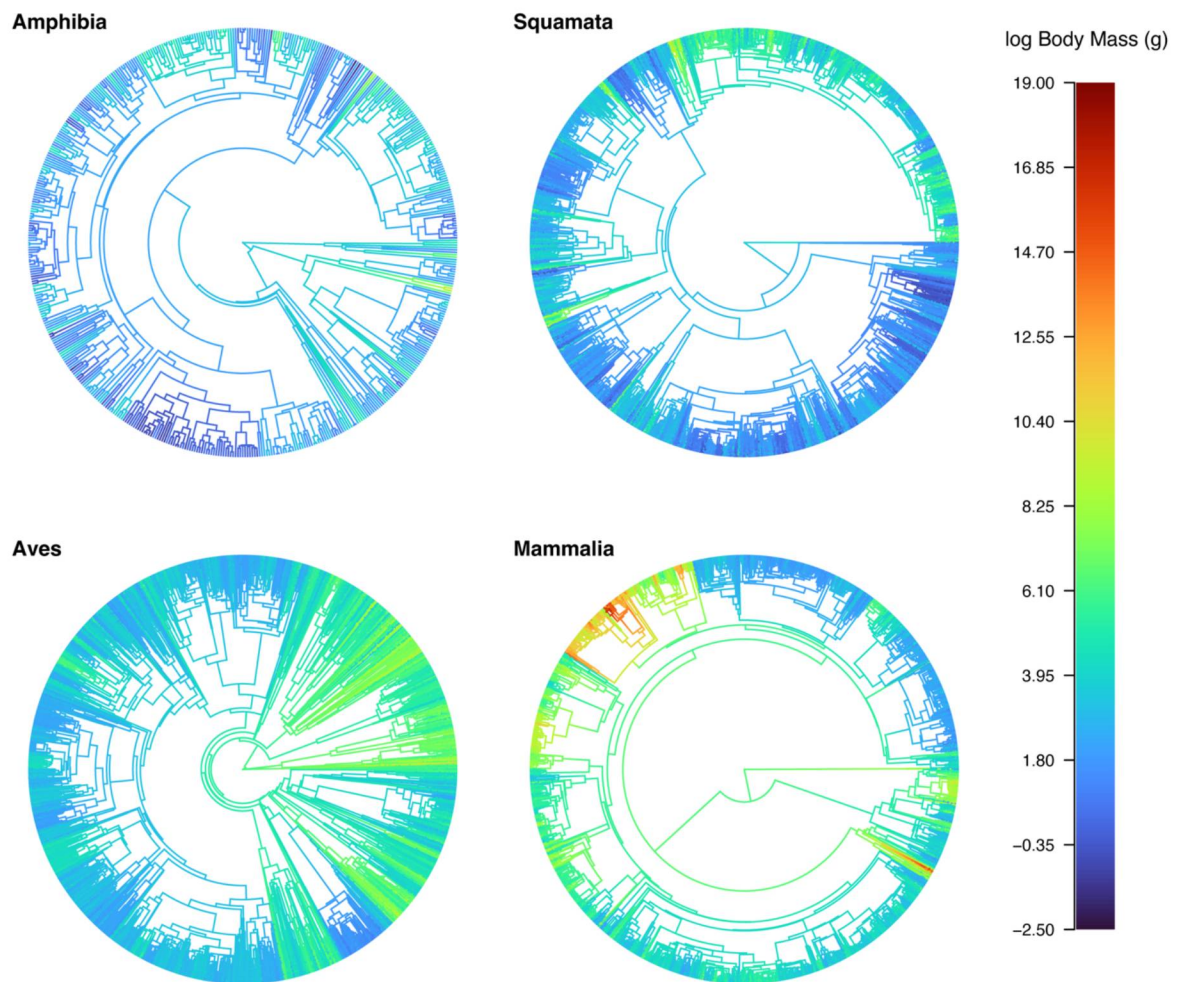
245

246 **Figure 2**. Character mapping and ancestral state reconstruction of body mass (g) for

247 amphibians, squamates, birds, and mammals.

248

249   There was substantial heterogeneity in evolutionary rates over time in all taxa, although

250 several periods did not depart from the null expectation (Figure 3). Amphibians and squamates

251 (Figures 3A,B) showed periods where the disparity accumulation was higher than expected,

252 with increases near the present. However, this was not the case for birds and mammals (Figures

253 3C, D), except for a slight increase in disparity around 94 Mya (calculated using the mean of

254 ages between topologies) for mammals. Yet, this increase was still close to the expectation

255 based on simulations. For birds, it is possible to note an abrupt decrease in disparification

256 around 78-90 Mya (Figure 3C). One can see a similar trend in mammals but with an increase

257 and a subsequent decline in disparity around 94 Mya (Figure 3D). The results using SVL for

258 amphibians and squamates showed different results (Appendix A: Figure A6). In amphibians,

259 the observed disparity is less than expected for a large part of their history, and there is a modest

260 increase near the present (Appendix A: Figure A6A). Although one still can notice this

261 acceleration towards the present, the conflicting results with body mass can be attributed to the

262 SVL dataset being considerably more comprehensive than the body mass dataset, providing a

263 more general view of body size evolution in the group. A similar tendency in squamates is seen

264 using body mass and SVL, but the difference between the expected and observed is more

265 pronounced (Appendix A: Figure A6B). Further, squamates exhibit an abrupt decrease in

266 disparification around 146-171 Mya (Appendix A: Figure A6B), which is smaller using body

267 mass data. This discrepancy can be attributed to the appearance of Serpentes (around 122-146

268 Mya), which have disproportionately long bodies and can bias the results.
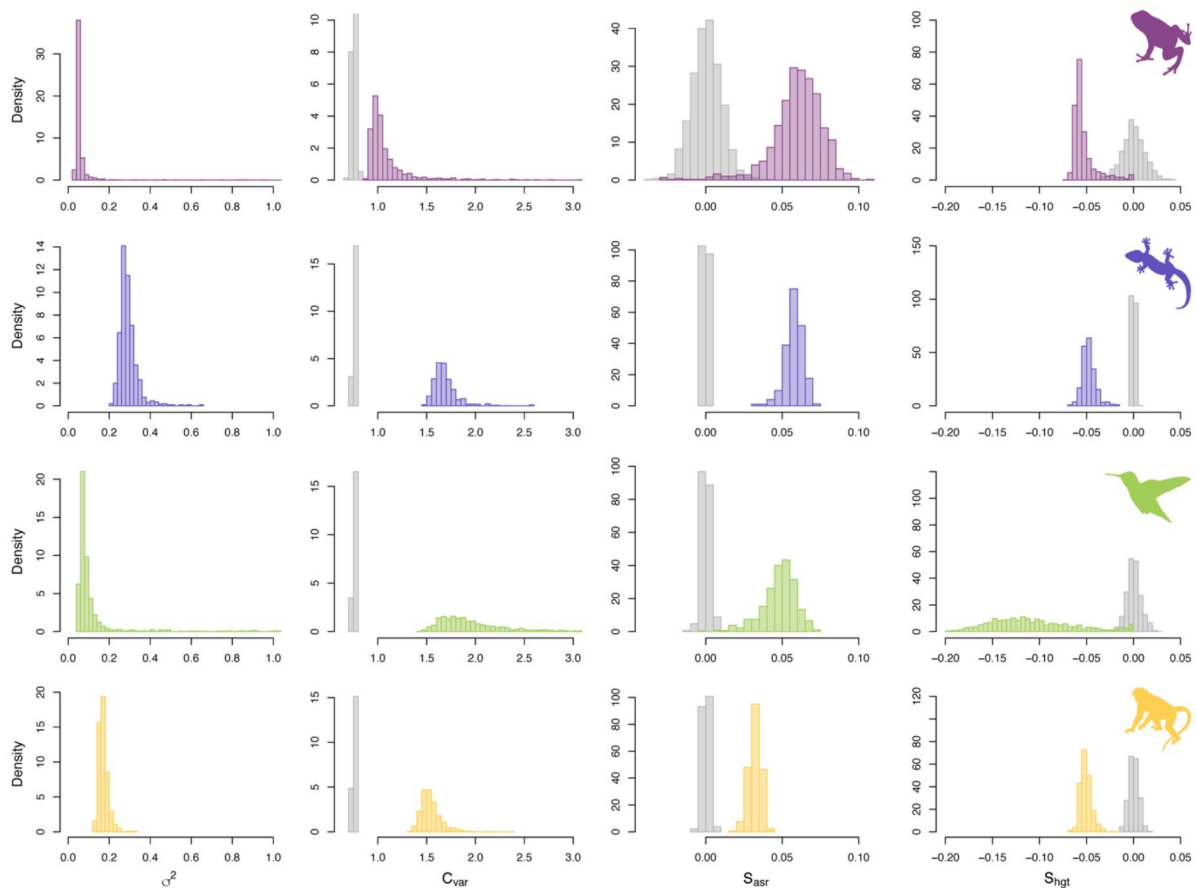
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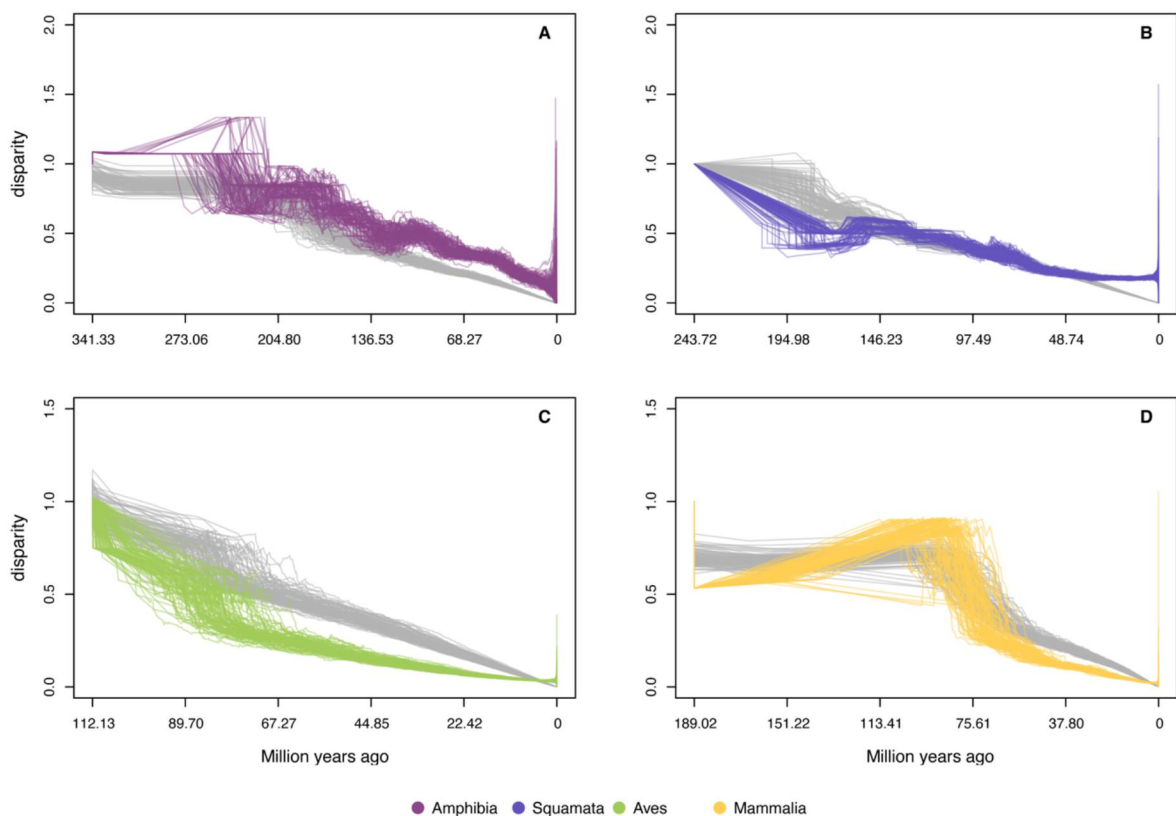
271 **Figure 3**. DTT (disparity-through-time) plots for body mass (g) for the studied taxa. Gray lines

272 indicate the null expectation under the Brownian Motion model of evolution, and color lines

273 correspond to the observed disparity variation in the empirical data. Estimates of body mass

274 were log-transformed before the analyses.

275

276   There was broad congruence across taxa in tests based on the model adequacy of a

277 constant-rate model, with all but one statistic consistently departing from data generated with

278 posterior predictive simulations in the same direction (Figure 4). The M_{sig} was the only statistic

279 in which the observed values did not differ from the expectation, indicating that the BM model

280 did not consistently over or underestimate the rates of evolution in these taxa. For this reason,

281 we only show the estimated evolutionary rates (σ^2) for each group (Figure 4) and not the

282 estimated mean of the squared contrasts. In general, amphibians and birds have similar

283 distributions of σ^2 for body size, with amphibians having a median of 0.050 and birds 0.077,

284 whereas squamates and mammals have higher median estimates of σ^2, with 0.284 for squamates

285 and 0.167 for mammals. Therefore, ectotherms and endotherms do not show consistent

286 differences in rates of evolution of body size. Interestingly, all taxa showed both C_{var} and S_{asr}

287 estimates that were higher than expected (Figure 4), which confirms that rate heterogeneity

288 exists across the phylogeny, as expected based on analyses shown in Figures 2 and 3. In

289 particular, these results regarding S_{asr} indicate that body size evolution is slower when the

290 ancestor is small and accelerates as the ancestor increases in size. In addition, all clades have

291 lower S_{hgt} values than expected, which indicates that the higher the node depth, the less contrast

292 in the trait, that is, the contrasts on the tips are higher than expected. Analyses using SVL were

293 very similar in deviating from the expected test statistics (Appendix A: Figure A7), but the

294 median values of σ^2 across topologies were 0.021 for amphibians and 0.033 for squamates.

295

Figure 4. Test statistics and evolutionary rates of body mass (g) generated using posterior predictive simulation. The first column corresponds to the rate of evolution under a Brownian Motion (BM) model for each taxon. C_{var} (coefficient of variation of the absolute value of the contrasts), S_{asr} (slope of a linear model fitted to the absolute value of the contrasts against the ancestral state inferred at the corresponding node), and S_{hgt} (slope of a linear model fitted to the absolute value of the contrasts against node depth) are indicated in the second, third, and fourth columns, respectively. Gray histograms are the null expectation under BM, and colored histograms are the statistics generated from the empirical data. Estimates of body mass were log-transformed before the analyses.

There was an overall correspondence between mean body mass and its evolutionary rate over geographical space within each clade, yet correspondence between clades was considerably less apparent (Figure 5). For instance, amphibians in the northern part of North

310   America, the southern part of South America, the southern part of Africa, Asia, and Western

311   Europe showed larger median body sizes and higher evolutionary rates (Figure 5). Similarly,

312   squamates exhibit similar patterns, with high values for body mass and evolutionary rates in

313   Asia and Europe, Brazil, central Africa, and northern North America (Figure 5). However, for

314   birds and mammals, there were differences between regions with large species and high rates

315   of evolution. Large bird species are predominantly found at high latitudes, including Australia,

316   northern North America, Europe, and Asia, as well as the southern part of South America.

317   Meanwhile, high rates of evolution are found in North Africa, parts of eastern Australia, and

318   Europe, but with a tendency towards the south (Figure 5). In contrast, large mammals and high

319   evolutionary rates are found in northern North America, southern South America, and western

320   Asia, while high evolutionary rates and larger species are found in North and South Africa and

321   central Africa, respectively (Figure 5). Finally, the geographical distribution of reptile snout-

322   to-vent length (SVL) exhibited similar patterns to their body mass (Appendix A: Figure A8).

323   However, amphibians showed a slightly different distribution of SVL, with most of those with

324   significant length and evolutionary rate concentrated in the Northern Hemisphere (Appendix

325   A: Figure A8). This incongruence between the two datasets is likely due to the limited

326   availability of body mass data for amphibians.

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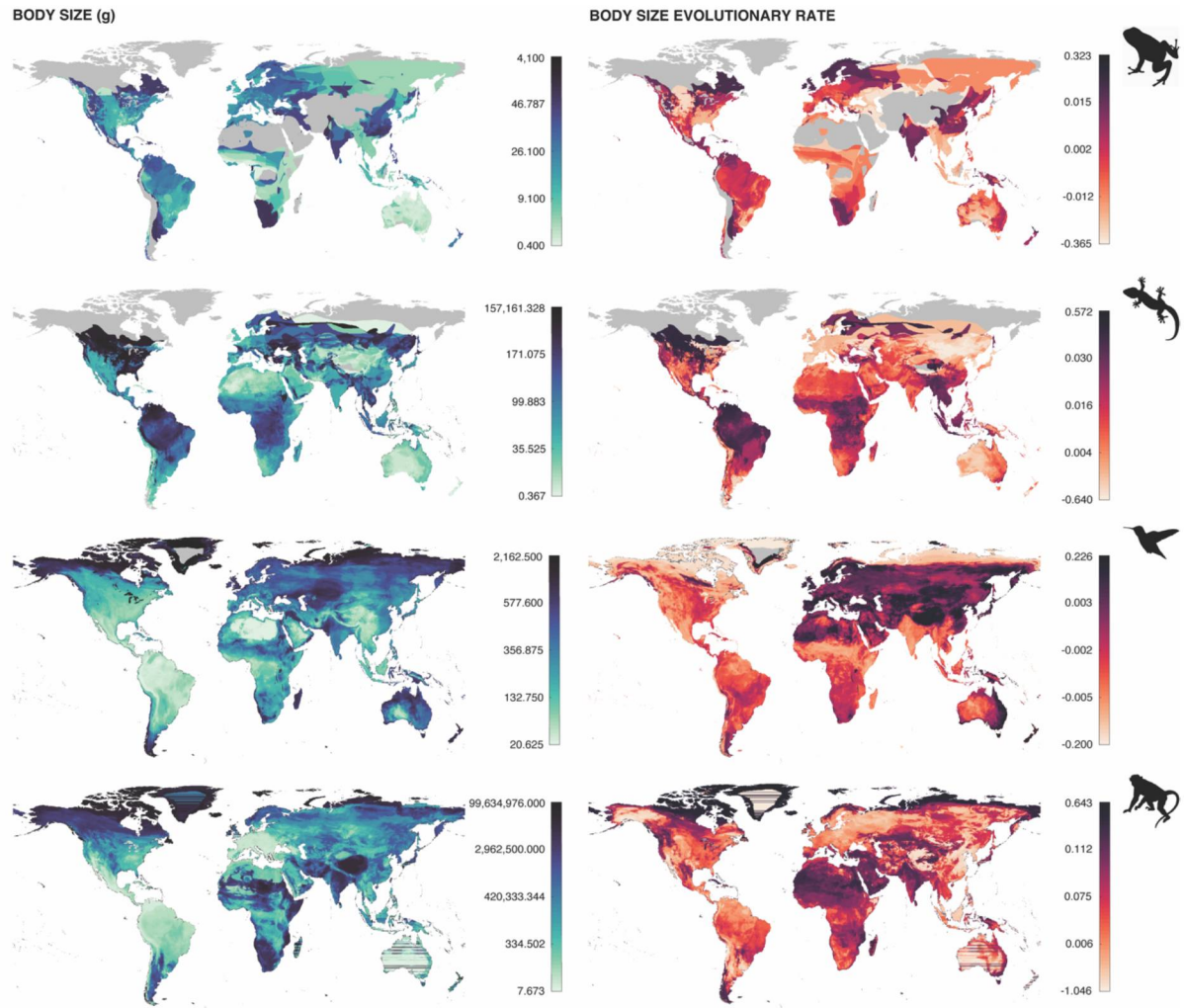
Figure 5. Geographical distribution of body mass (g) and the evolutionary rates of body mass (g) in each taxon studied. Both body mass and evolutionary rate were calculated as the median across all species within each cell.

4. Discussion

One would be hard-pressed to find a trait that is more consequential to so many aspects of the ecology, physiology, and evolution of an organism than its body size. Here, we provide a comprehensive exploration of body size evolution across terrestrial vertebrates. We found support for consistent departures from a constant-rate model across all clades (Figures 4; Appendix A: A7), suggesting that body size evolution may be characterized by similar rules across terrestrial vertebrates. In particular, they were characterized by rate heterogeneity

340   between lineages, accelerating rate of evolution with increasing body size, and more contrasts

341   than expected near the tips of the phylogenies (Figures 4; Appendix A: Figure A7).

342   Interestingly, although ectotherms tend to have smaller body sizes than endotherms (Figure 1),

343   their rates of evolution did not show substantial differences (Figure 4; Appendix A: Figure A7),

344   contrary to our initial expectations. Finally, although mean body size and rate of body size

345   evolution showed geographical congruence within clades, there was limited correspondence

346   between clades (Figures 5; Appendix A: A8), which might indicate that environmental drivers

347   such as mean annual temperature might not be sufficient to generate convergent patterns at

348   geographical scales. In aggregate, these results suggest that there might be common principles

349   governing body size evolution in terrestrial vertebrates, although their underlying mechanisms

350   are still poorly understood.

351   The results of our posterior predictive simulations showed evidence for a positive

352   relationship between body size and its rate of evolution in all tested clades (Figure 4).

353   Hutchinson (1959) previously discussed the notion that small and large species may undergo

354   distinct evolutionary processes due to the biased distribution of body sizes among species.

355   Building upon this idea, Baker et al. (2015) arrived at a similar conclusion, demonstrating a

356   positive relationship between evolutionary rate and body size when fitting branch-specific

357   evolutionary rates to diverse mammal lineages. Potential mechanisms explaining this pattern,

358   as proposed by Stanley (1979), include the relaxation of size-linked genetic or developmental

359   constraints, as well as the low population densities characteristic of larger species. However,

360   formal tests of these propositions are scarce (e.g., Baker et al., 2015; Cooper & Purvis, 2009).

361   Still, another perspective to consider is that small species may exhibit decreased rates of

362   evolution, instead of large mammals having increased rates. This alternative viewpoint could

363   be explained by a possible lower physiological limit on size (Stanley, 1973), which makes

364   evolution towards larger sizes more probable. Nevertheless, contrasting evidence from other

365 studies cannot be ignored. Some studies speculate that small-sized species can also have higher

366 evolutionary rates due to their faster life history (Bonner, 1965), while others find evidence that

367 certain groups exhibit high rates of evolution in both small and large animals, with intermediate

368 sizes showing lower rates (Cooper & Purvis, 2009). Nonetheless, our results indicate that

369 smaller species generate descendants with less variation in body size, but further examination

370 of lineages within terrestrial vertebrates may uncover different correlations and provide

371 additional insights into this relationship.

372 Regarding variation in time, our results are not consistent with an adaptive radiation

373 scenario in which body size evolution is faster early during the history of a clade and becomes

374 increasingly slower as ecological space is occupied (Simpson, 1944). Other studies obtained

375 similar results (Harmon et al., 2010b; Venditti et al., 2011). Instead, we show that there is

376 evidence for more contrast of body size near the present, and along with inspection of the DTT

377 plots, most of the histories do not differ from the expected under a time-homogeneous, constant

378 model of evolution. Although there are some deviations from the expected in each taxon, there

379 is not a general pattern that allows us to determine a single phenomenon generating these

380 deviations. In particular, one can say that the results of DTT plots and S_{hgt} statistics are

381 contradictory, for the former points to more disparity between clades than within clades, and

382 the latter indicates more contrast in the tips of the phylogenies. However, as the DTT plots show

383 much overlap with the expected and the S_{hgt} indicates slopes close to 0 (i.e., little to no linear

384 relationship between contrasts and node depth), we believe that the results are not conflicting.

385 The lack of a relationship between latitude and body size contradicts the expectations

386 set by existing hypotheses. Bergmann's rule and the water conservation hypothesis posit that

387 endotherms would tend to have larger body sizes at high latitudes to better conserve heat

388 (Bergmann, 1847), and ectotherms to conserve water (Nevo, 1973), respectively. On the other

389 hand, the heat balance hypothesis predicts that ectotherms would tend to have smaller sizes in

390   high latitudes due to their inability to self-produce heat, benefiting from reductions in size in

391   these locations (Olalla-Tarraga et al., 2006). Our results align with previous studies that also

392   did not find evidence for Bergmann's rule (e.g., Johnson et al., 2023; Pincheira-Donoso et al.,

393   2008; Womack & Bell, 2020), the water conservation hypothesis (e.g., Ashton & Feldman,

394   2003; Johnson et al., 2023; Servino et al., 2022), or the heat balance hypothesis (e.g., Johnson

395   et al., 2023; Slavenko et al., 2019; Slavenko & Meiri, 2015). An alternative interpretation of

396   these hypotheses could be that there is no latitudinal trend in body size, but rather in the rate of

397   evolution of these sizes. However, even the rates of evolution in our study do not support this

398   perspective. Overall, our findings contradict established hypotheses regarding the relationship

399   between latitude and body size, but instead suggest that there is a spatial association between

400   the average species mass of a region and its average evolutionary rate.

401   Although our results are consistent across a diversity of taxa, it is important to note some

402   caveats in our analyses. First, the model adequacy approach may indicate problems in the data.

403   For instance, as pointed out by Pennell et al. (2015), when both the S_{var} and the S_{hgt} statistics

404   show negative slopes in the observed data, it may be an indicator of problems in the estimated

405   branch lengths of the phylogeny, considering that S_{var} (not used here) would indicate errors in

406   branch lengths of shorter branches of the phylogeny and S_{hgt} would point to more contrasts in

407   the tips. However, we do not think this would be the case, given that all results were consistent

408   across 1000 alternative topologies and every taxon tested. Furthermore, previous studies have

409   demonstrated that ancestral state reconstruction using body size data might not be very accurate,

410   considering that most reconstruction methods assume a time-homogeneous process (Baker et

411   al., 2015). We do not believe this is a problem in the interpretation of the results, given that our

412   focus using this approach was not to determine the ancestor state but to visualize how body size

413   is distributed within the taxa.

414   In exploring differences in body size evolution in terrestrial vertebrates, we believe that

415   future studies may explore how differences in lineages within these clades are structured, using

416   data-driven approaches (e.g., Eastman et al., 2011; Thomas & Freckleton, 2012; Uyeda &

417   Harmon, 2014), for example. Once this is achieved, it can be interesting to build a causal model

418   to possibly explain how this heterogeneity is generated, using latitude or climate as explanatory

419   variables, and assess if the same variables have equal power to predict body size evolution

420   among terrestrial vertebrates. Thus, we hope that future studies would focus on describing how

421   other aspects of body size evolution may also be general across terrestrial vertebrates and if the

422   patterns uncovered here might be extended to other groups of organisms.

423

424   5.   Author Contributions

425   **Fernanda S. Caron**: Conceptualization (equal); data curation (equal); formal analysis

426   (equal); funding acquisition (equal); investigation (equal); methodology (equal); project

427   administration (equal); resources (equal); software (equal); validation (equal); visualization

428   (equal); writing – original draft (equal); writing – review & editing (equal). **Marcio R. Pie**:

429   Conceptualization (equal); project administration (equal); supervision (equal); writing – review

430   & editing (equal).

431

435

436   7.   Data Availability Statement

437   All the data utilized in our analyses were obtained from previous studies and are

438   accessible for public use.

439

8.   Competing Interests

The authors declare no competing interests.

442

443   **9.   References**

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634

635 **FIGURE LEGENDS**

636

637 **Figure 1**. Density distribution of body mass (g) in terrestrial vertebrates. Distributions are

638 shown for amphibians (A), squamates (B), birds (C), and mammals (D) separated by selected

639 subclades, and for the entire taxa (E). Lines in (E) indicate the median body mass for each

640 lineage. Body mass estimates for squamates, birds, and mammals were averaged across sources.

641

642 **Figure 2**. Character mapping and ancestral state reconstruction of body mass (g) for

643 amphibians, squamates, birds, and mammals.

644

645 **Figure 3**. DTT (disparity-through-time) plots for body mass (g) for the studied taxa. Gray lines

646 indicate the null expectation under the Brownian Motion model of evolution, and color lines

647 correspond to the observed disparity variation in the empirical data. Estimates of body mass

648 were log-transformed before the analyses.

649

650 **Figure 4**. Test statistics and evolutionary rates of body mass (g) generated using posterior

651 predictive simulation. The first column corresponds to the rate of evolution under a Brownian

652 Motion (BM) model for each taxon. C_{var} (coefficient of variation of the absolute value of the

653 contrasts), S_{asr} (slope of a linear model fitted to the absolute value of the contrasts against the

654 ancestral state inferred at the corresponding node), and S_{hgt} (slope of a linear model fitted to the

655 absolute value of the contrasts against node depth) are indicated in the second, third, and fourth

656 columns, respectively. Gray histograms are the null expectation under BM, and colored

657 histograms are the statistics generated from the empirical data. Estimates of body mass were

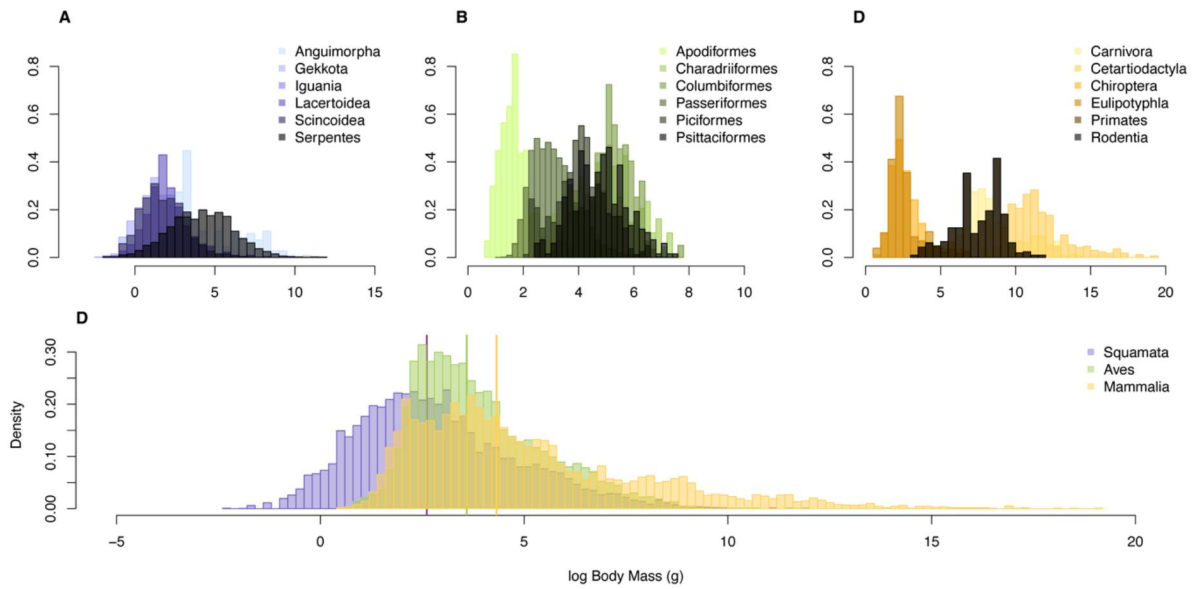658 log-transformed before the analyses.

659

660   **Figure 5**. Geographical distribution of body mass (g) and the evolutionary rates of body mass

661   (g) in each taxon studied. Both body mass and evolutionary rate were calculated as the median

662   across all species within each cell.

663

664

665

666

Figure A1. Density distribution of body mass (g) for terrestrial vertebrates. Distributions are

shown for squamates (A), birds (B), and mammals (C) separated by selected subclades, and for

the entire taxa (D). Lines in (D) indicate the median body mass for each lineage. Body mass

estimates are the median across sources.
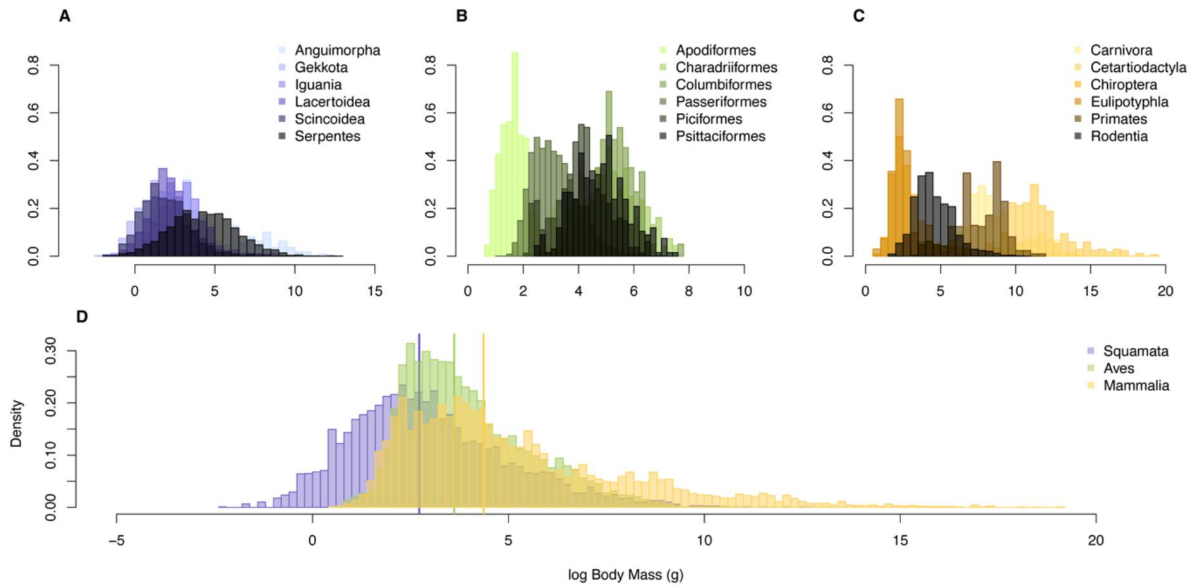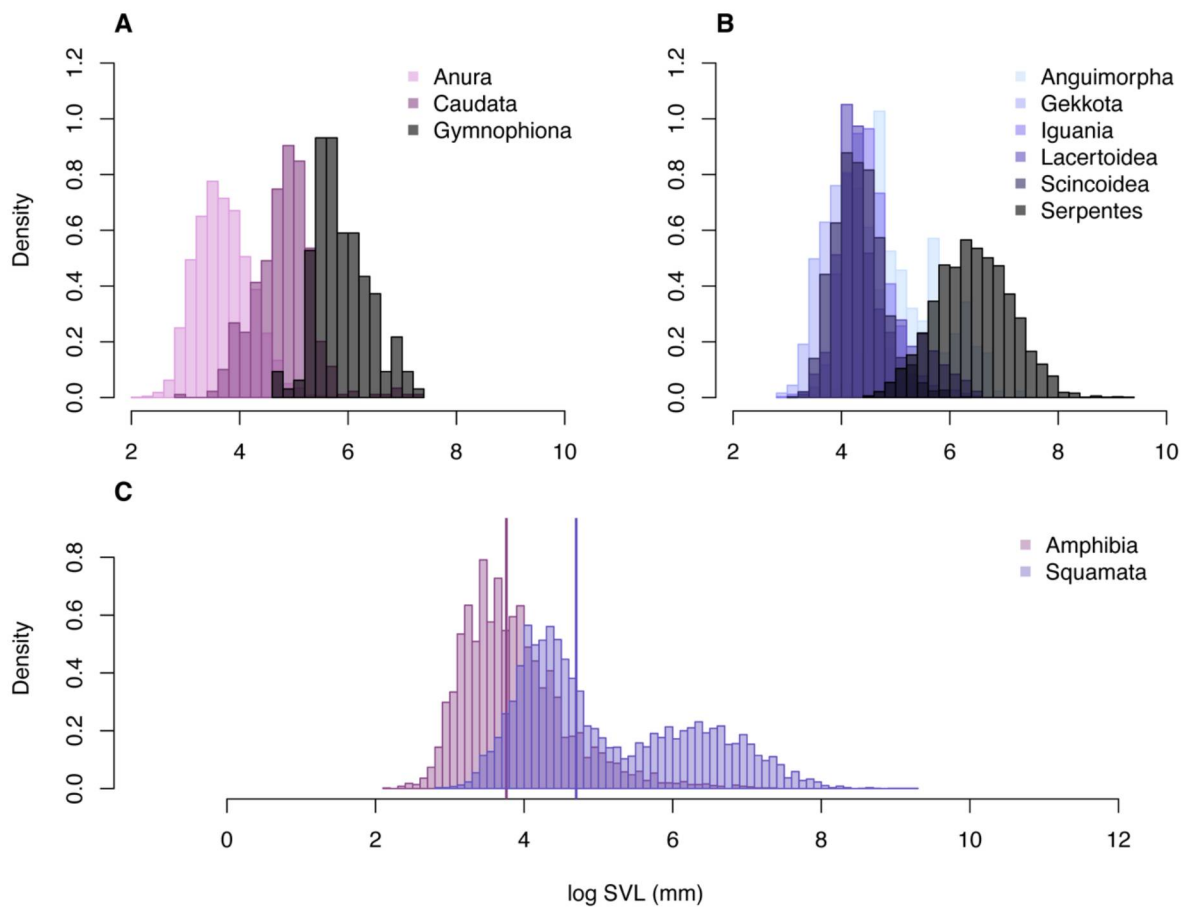
671

Figure A2. Density distribution of body mass (g) for terrestrial vertebrates. Distributions are shown for squamates (A), birds (B), and mammals (C) separated by selected subclades and for the entire taxa (D). Lines in (C) indicate the median body mass for each lineage. Body mass estimates are the maxima across sources.
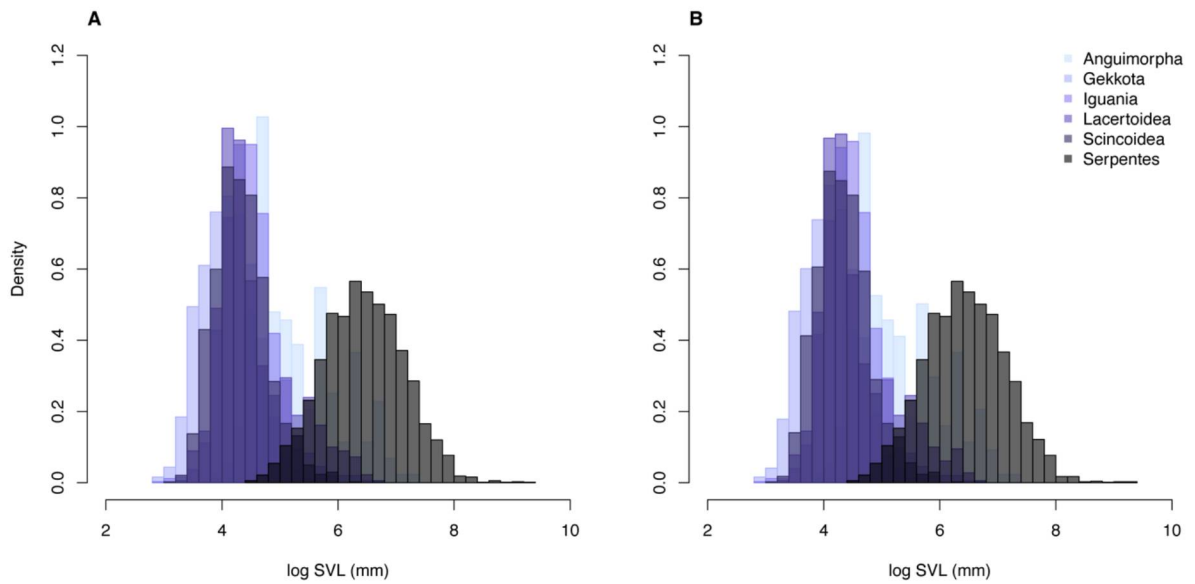
Figure A3. Density distribution of snout-vent length (SVL) (mm) for terrestrial ectotherms. Distributions are shown for amphibians (A), and squamates (B) separated by selected subclades, and for the entire taxa (C). Lines in (C) indicate the median body mass for each lineage. Body mass estimates for squamates are the average across sources.

684

685   **Figure A4**. Density distribution of snout-vent length (SVL) (mm) for squamates. Distributions

686   are separated by selected subclades (A and B), and for the entire taxa (C). Lines in (C) indicate

687   the median body mass for each lineage. Body mass estimates for squamates are the median (A),

688   and the maximum (B) across sources, and in C are the density distributions comparing both

689   approaches.

690
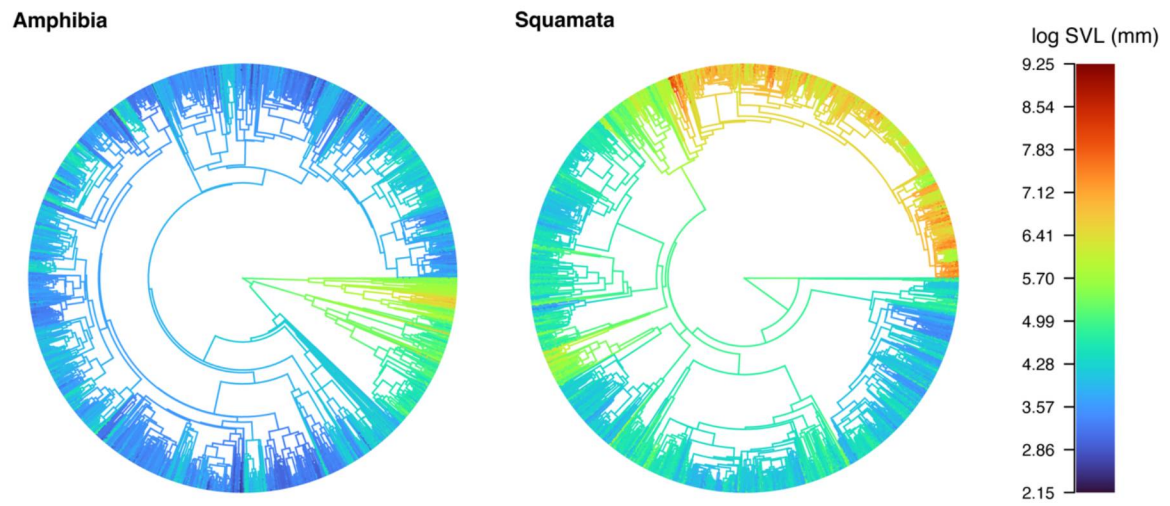
691

692 **Figure A5**. Character mapping and ancestral state reconstruction of snout-vent length (SVL)

693 (mm). A. amphibians, and B. squamates.
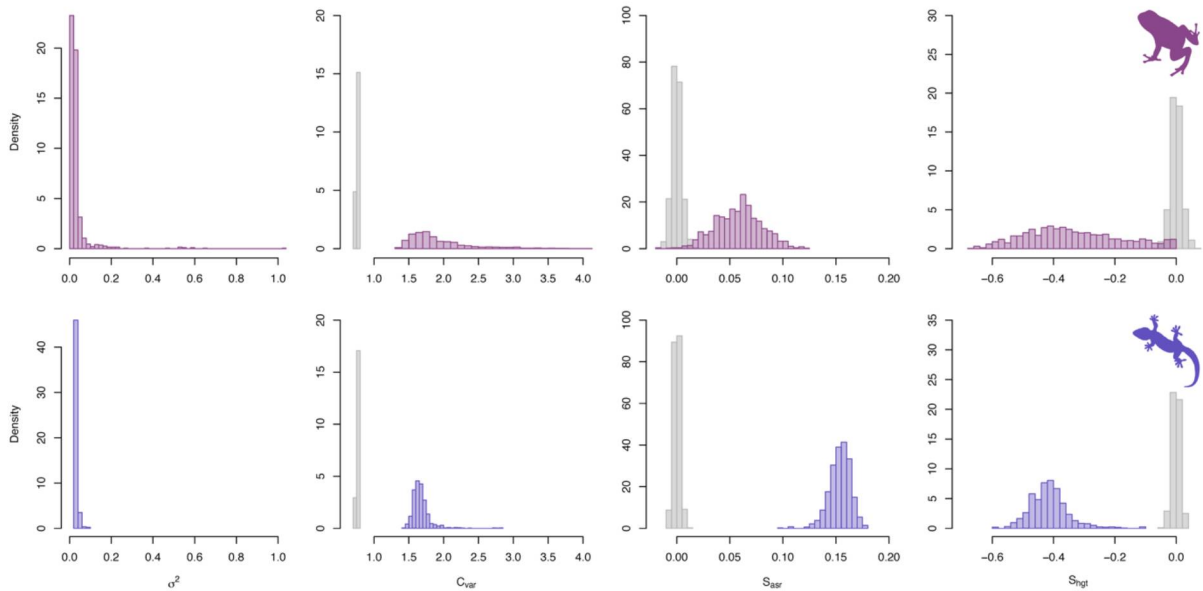
694
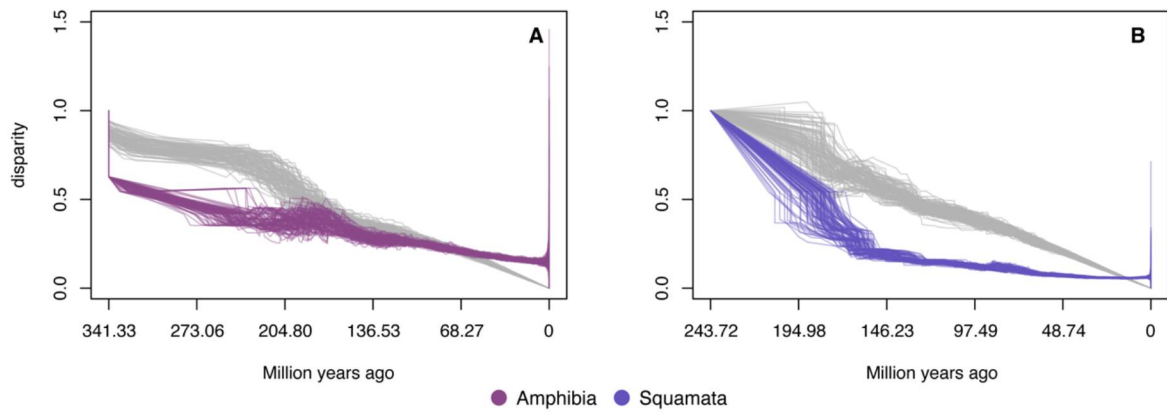
Figure A6. DTT (disparity-through-time) plots for snout-vent length (SVL) (mm). A. amphibians, and B. squamates. Gray lines indicate the null expectation under the Brownian Motion model of evolution and color lines correspond to the observed disparity variation in the empirical data. Estimates of body mass were log-transformed before the analysis.

Figure A7. Test statistics and evolutionary rates of snout-vent length (SVL) (mm) generated using posterior predictive simulation. The first column corresponds to the rate of evolution under a Brownian Motion (BM) model for each taxon. Cvar (coefficient of variation of the absolute value of the contrasts), Sasr (slope of a linear model fitted to the absolute value of the contrasts against the ancestral state inferred at the corresponding node), and Shgt (slope of a linear model fitted to the absolute value of the contrasts against node depth) are indicated in the second, third, and fourth columns, respectively. Gray histograms are the null expectation under BM, and colored histograms are the statistics generated from the empirical data. Estimates of body mass were log-transformed before the analysis.

712

713 **Figure A8**. Geographical distribution of snout-vent-length (SVL) (mm) and the evolutionary

714 rates of SVL in each taxon studied. Both SVL and evolutionary rate were calculated as the

715 median across all species within each cell.

716

CAPÍTULO II

THE MACROEVOLUTION OF SEXUAL SIZE DIMORPHISM IN BIRDS

Capítulo em formato de artigo de acordo com as normas para submissão da revista *Biological Journal of Linnean Society*, mas com as figuras e tabelas inseridas no texto para facilitar a leitura.

1   **The macroevolution of sexual size dimorphism in birds**

2

3 **Abstract**

4 The degree of sexual size dimorphism (SSD) varies considerably among animal groups, yet the

5 drivers of interspecific variation in SSD are still poorly understood. Possible mechanisms have

6 been suggested, including sexual selection, selection for fecundity in females, niche divergence

7 between sexes, and allometry, yet their relative importance is still poorly understood. In this

8 study, we test predictions of these four hypotheses in different avian groups using a large-scale

9 dataset on SSD for 4,761 species. Specifically, we estimated transition probabilities between

10 male- and female-biased SSD, tested for differences in evolutionary rates of body size evolution

11 for males and females, and assessed the potential ecological and spatial correlates of SSD. Our

12 results were consistent with the sexual selection, fecundity, and niche divergence hypotheses,

13 but their support varied considerably among avian orders. In addition, we found little evidence

14 that the direction of SSD affected the evolution of male or female body size, and no relationship

15 was detected between SSD and environmental predictors (i.e., temperature and precipitation

16 seasonality, productivity, species richness, and absolute latitude). These results suggest that

17 avian SSD evolution is likely to be multifactorial, with sexual selection, fecundity, and niche

18 divergence playing important roles in different avian orders.

19 **Keywords**: body size; evolutionary rates; phylogenetic comparative methods; sexual selection.

20

21   **1.   Introduction**

22   The degree of sexual size dimorphism (SSD) varies greatly across animal species, even

23   among closely-related taxa (e.g., Nuñez-Rosas *et al.*, 2017; Agha *et al.*, 2018; Portik,

24   Blackburn, & McGuire, 2020). For instance, female-biased SSD is common in invertebrates

25   and ectothermic vertebrates, such as the blanket octopus *Tremoctopus violaceus*, where females

26   can reach up to 40,000 times the weight of the male (Norman *et al.*, 2002). On the other hand,

27   male-biased SSD is prevalent in birds and mammals, such as elephant seals where males can

28   weigh up to 10 times more than females (Ralls & Mesnick, 2009). While extreme SSD occurs

29   relatively rarely, moderate SSD (e.g., when the sexes differ by less than 10%) is widespread

30   across various animal taxa (Fairbairn, Blanckenhorn, & Székely, 2007). Despite this

31   prevalence, the mechanisms that generate and maintain SSD are still poorly understood.

32   Although many mechanisms have been proposed as potential drivers of SSD evolution,

33   they can be tentatively summarised into four main hypotheses. According to the sexual selection

34   hypothesis, SSD could result from male-male competition, given that larger males could be

35   favoured in the context of female choice or direct combat (Székely, Reynolds, & Figuerola,

36   2000; Székely, Lislevand, & Figuerola, 2007; Owen *et al.*, 2017). Alternatively, the fecundity

37   hypothesis posits that SSD may be due to selection towards larger females for greater

38   reproductive capacity (Darwin, 1874; Reeve & Fairbairn, 1999; Székely *et al.*, 2007), which

39   might be enhanced in regions with shorter breeding seasons (Tarr *et al.*, 2019). In the niche

40   divergence hypothesis, SSD would be associated with ecological factors, such that differences

41   among sexes would result in resource partitioning, allowing for the exploitation of distinct

42   niches by males and females and leading to decreased intraspecific competition (Darwin, 1874;

43   Selander, 1966; Shine, 1994). Finally, the allometry hypothesis suggests a more structuralist

44   explanation for SSD based on Rensch's rule (i.e., male-biased SSD increases and female-biased

45   SSD decreases, with body size; Rensch, 1950, 1959). In particular, if SSD is strongly allometric,

46   selection for increased or decreased body size could indirectly lead to variation in SSD as a by-

47   product. Traditionally, previous studies tended to focus on only one of these hypotheses at a

48   time (but see Shine, 1994; Cox, Skelly, & John-Alder, 2003; Serrano-Meneses & Székely,

49   2006; Lislevand, Figuerola, & Székely, 2009; Stephens & Wiens, 2009; García-Navas *et al.*,

50   2016). These studies typically used proxies related to sexual selection, such as contrasting

51   mating systems and parental care (e.g., Horne, Hirst, & Atkinson, 2020; Gonzalez-Voyer *et al.*,

52   2022), or related to the fecundity hypothesis by measuring egg and clutch sizes (e.g., Serrano-

53   Meneses & Székely, 2006; Liang, Meiri, & Shi, 2022).

54   Our approach in this study differs from previous work in two main ways. First, we test
55 all four of these hypotheses within a similar, comparable framework, and a comprehensive
56 dataset involving information on thousands of species. Second, we explore predictions from
57 each hypothesis using an explicitly macroevolutionary approach (Table 1). For instance, given
58 that the sexual selection hypothesis implies that differences in SSD would be largely driven by
59 changes in male body size, one could predict that (1) transitions from female-biased SSD to
60 male-biased SSD should be more likely than in the other direction, and (2) the rate of male body
61 size evolution would be higher than the rate of female body size evolution. Likewise, the same
62 argument could be made for the fecundity hypothesis, but with opposite predictions, as SSD
63 would be driven largely by changes in female body size. On the other hand, as the niche
64 divergence hypothesis only predicts character displacement, it would not predict changes
65 preferentially in one of the sexes, thus both transition rates and rates of evolution should be
66 similar between males and females. Finally, given that either one or the other sex would depart
67 more markedly from the isometry line according to the allometry hypothesis, the rate of body
68 size evolution should be faster in whatever sex has the largest body size, whereas it makes no
69 clear prediction regarding differences in transition rates. We also explored ecological
70 predictions of different hypotheses, given that the fecundity hypothesis predicts a positive
71 relationship between female-biased SSD and seasonality (see Tarr *et al.*, 2019), whereas the
72 niche divergence hypothesis predicts a positive relationship between absolute SSD and species
73 richness and productivity, given that they would reflect local opportunity for interspecific
74 competition. Finally, if one envisions a scenario in which body size evolution is strongly
75 affected by latitude (i.e., Bergmann's rule; Bergmann, 1847), changes in SSD could be a by-
76 product of latitudinal variation in overall body size, so that absolute SSD values should be
77 positively correlated with latitude in the allometry hypothesis (Table 1). We focused on birds
78 as our model system for this study, given the extensive availability of data on their species
79 diversity, distribution, and body size.
80
81 **Table 1**. Predictions of the four hypotheses tested in the present study as potential drivers of
82 SSD. See text for details.

Hypothesis	Transitions between types of SSD	Rates of body mass evolution	Spatial/ecological correlates

Sexual selection	♂ SSD → ♀ SSD < ♀ SSD → ♂ SSD	Rate of ♂ > Rate of ♀	No clear prediction
Fecundity	♂ SSD → ♀ SSD > ♀ SSD → ♂ SSD	Rate of ♂ < Rate of ♀	Positive relationship between ♀ SSD and seasonality
Niche divergence	♂ SSD → ♀ SSD ≈ ♀ SSD → ♂ SSD	Rate of ♂ ≈ Rate of ♀	Positive relationship between absolute SSD and species richness + productivity
Allometry	No clear prediction	Rate of body size evolution should be faster in the larger sex	Positive relationship between absolute SSD and latitude

2.   Materials and Methods

2.1.   Data Sources

Body mass data for males and females of a total of 4,761 bird species were obtained from Lislevand *et al.* (2007), Myhrvold *et al.* (2015), and Ocampo *et al.* (2021). We focused our analyses on the nine most species-rich orders, namely Accipitriformes, Anseriformes, Apodiformes, Charadriiformes, Columbiformes, Galliformes, Passeriformes, Piciformes, and Psittaciformes. When a species was present in more than one source, the average of the corresponding estimates was used in subsequent analyses (for the complete compiled dataset, see Supplementary Table S2). Phylogenetic relationships were retrieved from Jetz *et al.* (2012) (Ericson backbone trees). Species distribution data were obtained from the BirdLife International database (BirdLife International and Handbook of the Birds of the World, 2021). Finally, bioclimatic data was retrieved from WorldClim (Fick & Hijmans, 2017) and net primary productivity (NPP) data were extracted from Sun et al.(Sun *et al.*, 2020). To analyze the NPP data, due to computational limitations, we averaged only the estimates of the last 10 years of the 38 years from Sun *et al.* (2020).

101   *2.2.   Analyses*

102   Sexual size dimorphism was measured according to the size dimorphism index (SDI) of

103 Lovich & Gibbons (1992), which is calculated as the ratio of the size of the larger sex in relation

104 to the smaller sex - 1, made arbitrarily negative if the male is larger and positive if the female

105 is larger. This measure of SSD is symmetric around zero, does not asymptote, and contains

106 information on direction, giving it desirable properties as a measure of SSD (Lovich & Gibbons,

107 1992). We mapped SDI and the log10-transformed average body size of each species onto the

108 phylogeny to explore how these traits are distributed across taxa, using the *phytools* v1.0-3

109 package (Revell, 2012). In this analysis, SDI was characterised as -1 if the species have male-

110 biased SSD or 1 if the species have female-biased SSD, disregarding the degree of SSD for

111 visualisation purposes. We also explored geographical variation in male- and female-biased

112 SSD by mapping the median SDI across all species present in a given cell at a 10-arc-minute

113 resolution. Maps were generated either using all species or separately only for species with

114 male- and female-biased SSD.

115   To test for asymmetry in the transition rates between female-biased SSD and male-

116 biased SSD, we fitted Mk models of discrete character evolution to our data. SDI was treated

117 as a binary variable, where -1 corresponded to male-biased SSD and 1 to female-biased SSD.

118 To simplify parameter estimation and model selection, monomorphic species (i.e., males and

119 females having exactly the same size) were excluded from this analysis (N=177, which

120 accounted for approximately 3.72% of the entire dataset). Including a third discrete state for

121 monomorphic species would considerably increase the complexity of the analysis, including

122 the comparison of non-nested models, making model comparisons challenging. A symmetrical

123 model, in which forward and backward rates are the equivalent, and an all-rates different model

124 were fitted to the data using the function fitMk from *phytools* v1.0-3 (Revell, 2012) and

125 evaluated according to their AICw. We used the package *AICcmodavg* v.2.3-1 (Mazerolle,

126 2020) to calculate AICw values and transition rates by averaging the estimates calculated for

127 each model. A common concern is that an association between character states with

128 diversification rates might bias transition rate estimates (Goldberg & Igić, 2008). To mitigate

129 this potential bias, we tested for an association between SSD and diversification rates, using a

130 semi-parametric test for trait-dependent diversification analyses (Harvey & Rabosky, 2018),

131 named "ES-sim" (available at https://github.com/mgharvey/ES-sim), which uses a tip-specific

132 metric λ_{DR} as a measure of diversification rate. Parametric state-dependent diversification

133 methods were not chosen due to their high rates of false-positive results (Beaulieu & O'Meara,

134   2016), and because simulations using ES-sim showed similar to or higher power than QuaSSE

135   (Harvey & Rabosky, 2018).

136   To determine whether divergent rates of evolution between male and female sizes are

137   causing the SSD, evolutionary rates were estimated using the function mvBM from the

138   *mvMORPH* v1.1-4 package (Clavel, Escarguel, & Merceron, 2015). Two alternative models

139   were tested according to constraints on evolutionary rates, in which the σ^2 from a Brownian-

140   Motion model were either the same between states (male or female body mass) or allowed to

141   differ. A loglikelihood-ratio test was then applied to determine the best-fitting model. Another

142   method for testing evolutionary rate variation and shifts in SSD evolution was applied, named

143   RRphylo, which is based on phylogenetic ridge regression (Castiglione *et al.*, 2018). As a first

144   step, we used the auto-recognize feature of the search.shift function from the *RRphylo* v2.6-0

145   package (Castiglione *et al.*, 2018) to identify any shifts in the degree of SSD across the

146   phylogenies of each order. Secondly, we applied the status type "sparse" of the function

147   search.shift to the evolution of male and female body mass, separately, and evaluate if their

148   rates of evolution differ when SDI was positive (female-biased SSD) or negative (male-biased

149   SSD). This allows us to test if the evolution of body size in each sex is affected by the direction

150   of dimorphism.

151   We tested for geographical correlates of SDI by extracting bioclimatic data (temperature

152   seasonality, precipitation seasonality, and net primary productivity) and latitude centroid for

153   each species based on their corresponding shapefiles and calculating species means at a

154   resolution of 10-arc-minutes. We performed a multiple phylogenetic least-squares regression

155   (PGLS) with the SDI of each species as the dependent variable and temperature seasonality,

156   precipitation seasonality, species richness (of the same order), NPP, and absolute latitude as

157   independent variables. We chose not to include any interaction terms in our model due to the

158   lack of prior expectations regarding their effects SSD. This decision was made to prevent a

159   significant increase in model complexity due to the large number of predictors, which would

160   have made the interpretation of results more challenging. All analyses in this study were

161   performed in R 4.2.0 (R Core Team, 2023) and repeated for 100 alternative topologies (1000 in

162   the case of PGLS) to account for phylogenetic uncertainty. Transition rates, evolutionary rates,

163   and PGLS were estimated separately for each studied order.

164

165   **3.   Results**

166   Different avian orders vary considerably in their distribution of body sizes, both in their
167   mean and degree of skewness, yet the shape of the distributions of male and female body sizes
168   remain relatively similar within each order (Fig. 1). Overall, Apodiformes and Passeriformes
169   show the lowest body mass of all orders (median of 5.2 and 21.456 g, respectively), whereas
170   Anseriformes and Accipitriformes have the highest masses (median of 896.562 and 670 g,
171   respectively). The degree of SSD varies substantially among species, ranging from -5.28 (the
172   male being 528% larger than the female) to 1.5 (the female being 150% larger than the male).
173   Altogether, 31.15% of the species across the nine studied orders show female-biased SSD,
174   whereas 65.13% of the species show male-biased SSD, and only 3.72% are monomorphic. The
175   majority of the orders (seven out of nine) have predominantly negative (male-biased SSD) SDI,
176   whereas the remaining two (Accipitriformes and Charadriiformes) tend to have positive SDIs
177   (Fig. 2). The orders showing the most disproportionate frequency of species with only one type
178   of SDI were Accipitriformes, with 95% of their species with positive SDI, and Anseriformes,
179   with 91% of their species with negative SDIs.

180

181
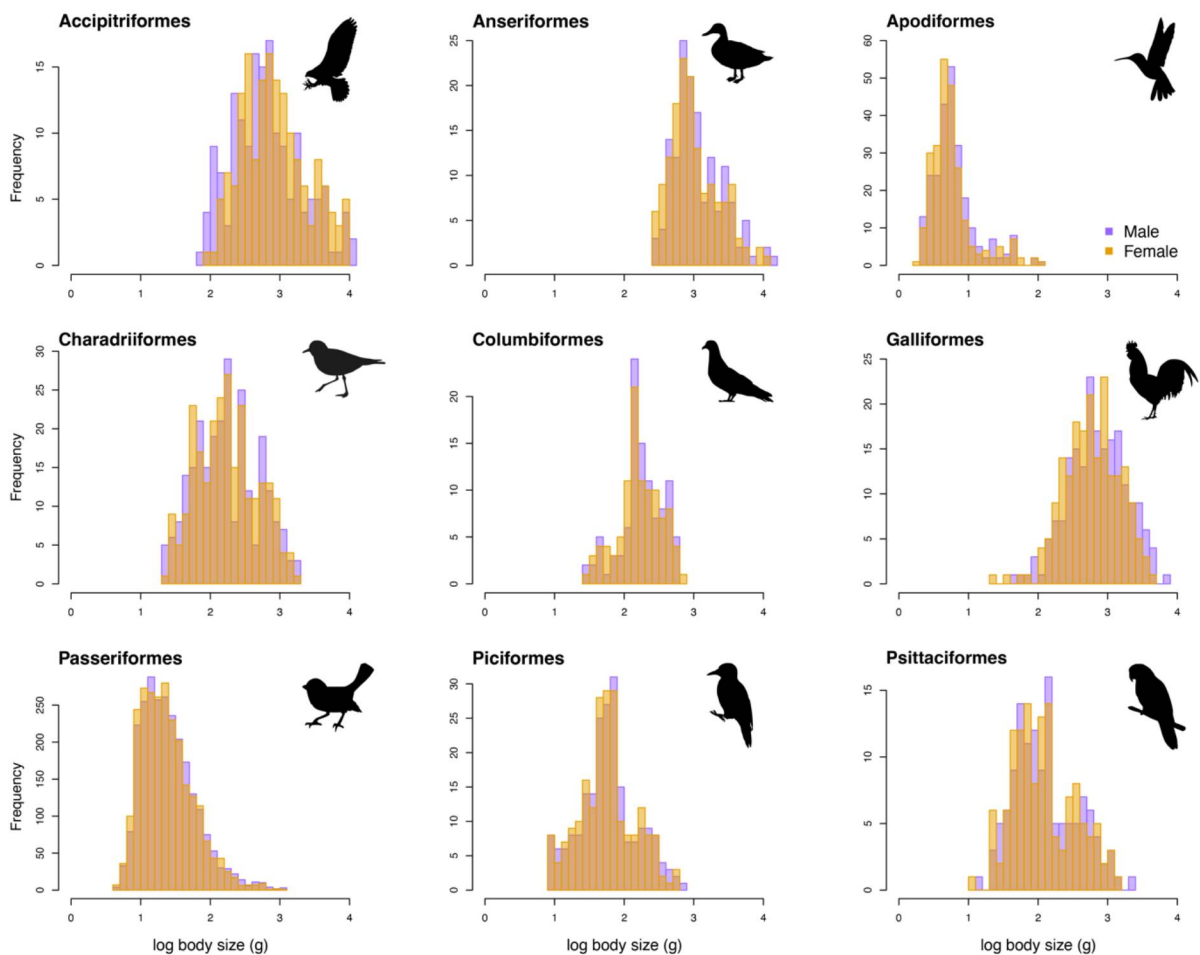
182 **Figure 1.** Frequency distributions of body mass (g) across the nine studied orders. Within each

183 order, different colours represent the distribution of each sex. Values were ln-transformed prior

184 to visualization.

185
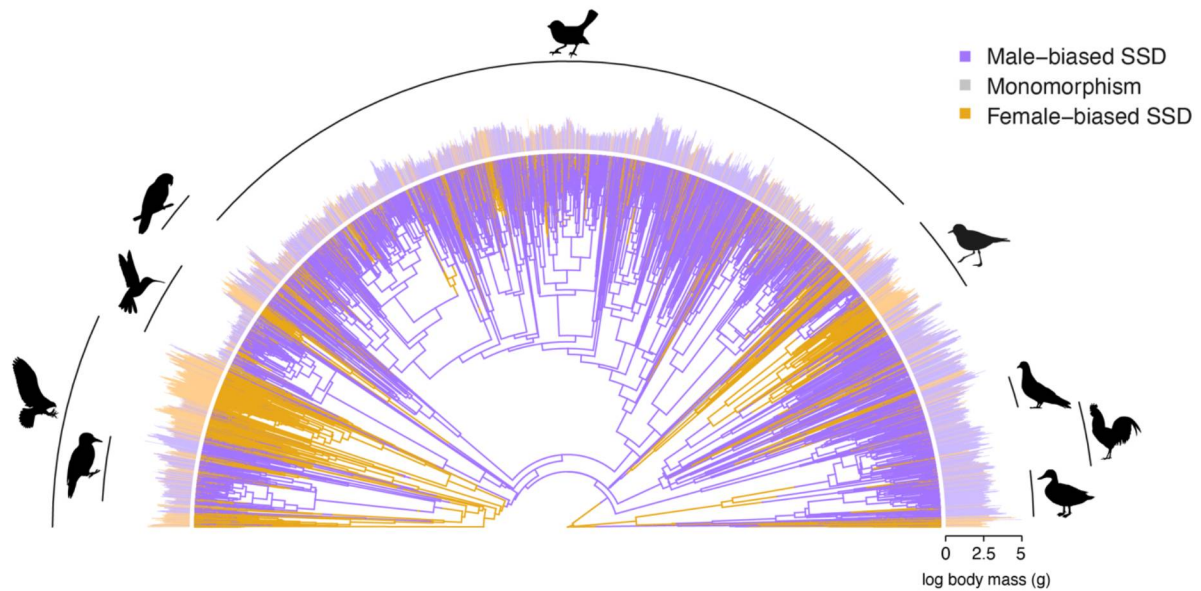
186

187 **Figure 2.** Stochastic character mapping of sexual size dimorphism coded as male-biased,

188 female-biased, or monomorphic. Bars at the top of the phylogeny tips correspond to log body

189 mass (g) of each species, calculated as the average of the male and female body mass. As shown

190 in Fig. 1, the nine orders selected for the present study are represented by arcs with their

191 respective silhouettes.

192

193　　There are intriguing differences in the geographical distribution of male- and female-

194 biased SSD (Fig. 3). The first map indicates the spatial distribution of SSD, as measured by the

195 median absolute SDI of all species in each cell (Fig. 3A). Given that it uses the absolute SDI

196 values, this map describes spatial variation in the degree of SSD, regardless of whether it is

197 male- and female-biased. There is a relatively loose association between SSD and overall

198 environmental conditions. In the New World, SSD is less pronounced in the humid tropics of

199 South and Central America (yet considerably stronger in the humid forests of Africa), but also

200 in the dry conditions of northern Africa and the Middle East, and the temperate climates of

201 Eurasia (Fig. 3A). On the other hand, high SSD is found both at high latitudes, but also in more

202 mesic conditions in SE Asia and Eastern Australia (Fig. 3A). Interestingly, male-biased SSD

203 tend to follow closely the same geographical patterns as the absolute SDIs, except for a

204 relatively higher intensity in Sub-Saharan Africa (Fig. 3B). However, this observation could be

205   attributed to the fact that more than half of the species in our dataset (65%) display male-biased

206   SSD. Female-biased SSD, however, shows important differences from the overall geographical

207   distribution of SSDs, with disproportionately higher values, especially throughout northern

208   Eurasia and northern Australia (Fig. 3C).

209

(a) **All species**
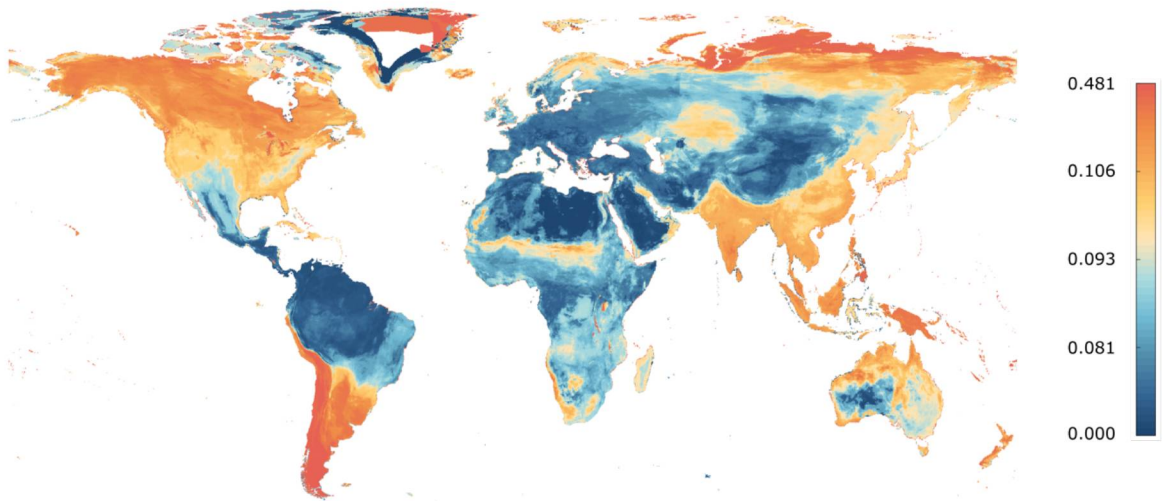
(b) **Male-biased SSD**
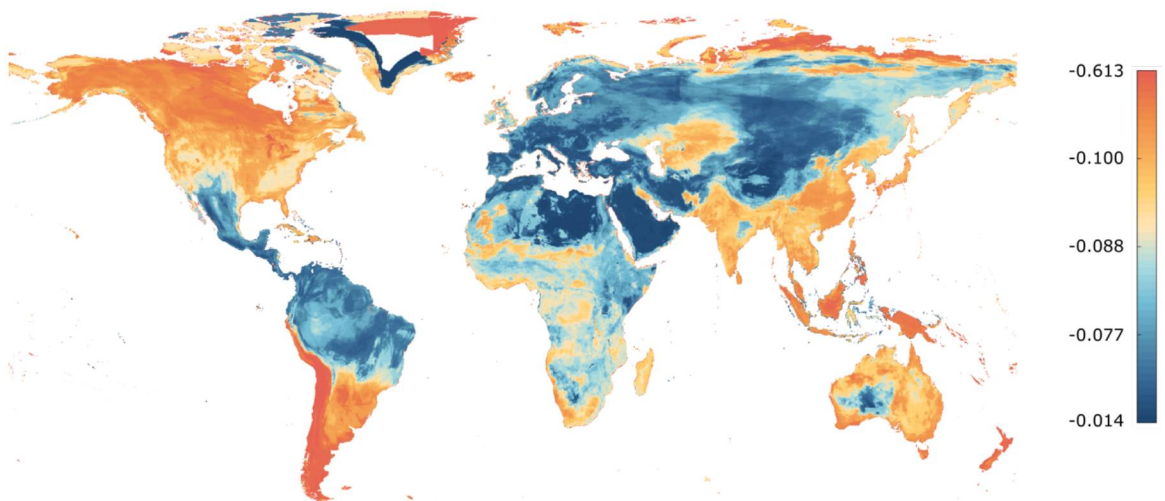
(c) **Female-biased SSD**
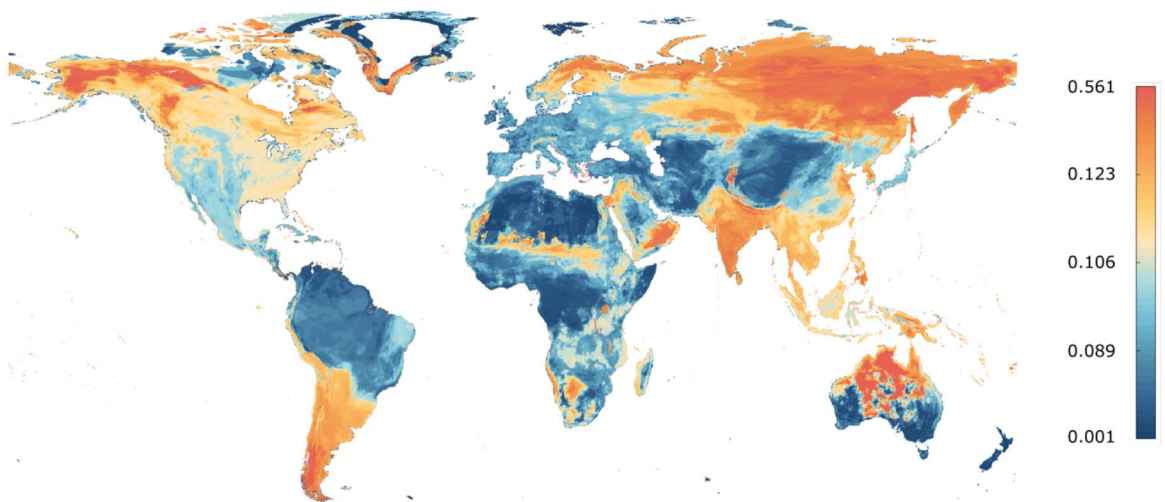
210

211 **Figure 3.** Geographic distribution of avian sexual size dimorphism. SSD was measured by the

212 index of Lovich & Gibbons (1992). A. Median value across all species found on each cell; B.

213   median values considering only species with male-biased sexual size dimorphism (SSD); C.

214   median values considering only species with female-biased SSD.

215

216   The analysis of transition rates shows that transitions from female-biased SSD to male-

217   biased SSD are more likely than the reverse (Fig. 4). This pattern is apparent in Apodiformes,

218   Columbiformes, Galliformes, Passeriformes, Piciformes, and Psittaciformes, all of which

219   showed a predominance of male-biased SSD. Conversely, Accipitriformes and Charadriiformes

220   show higher transition rates from male-biased SSD to female-biased SSD than the reverse—

221   interestingly, the only two orders analysed here which have more species with female-biased

222   SSD. Finally, Anseriformes is the only order in which the symmetrical model is preferred

223   according to the AIC (Table 2). It is important to note that these results are unlikely to have

224   been due to an association between the character states and diversification rates, given that our

225   analyses using λ_{DR} do not show any association between them (Fig. 5; $p > 0.05$ for 100

226   simulations for each alternative topology).

227
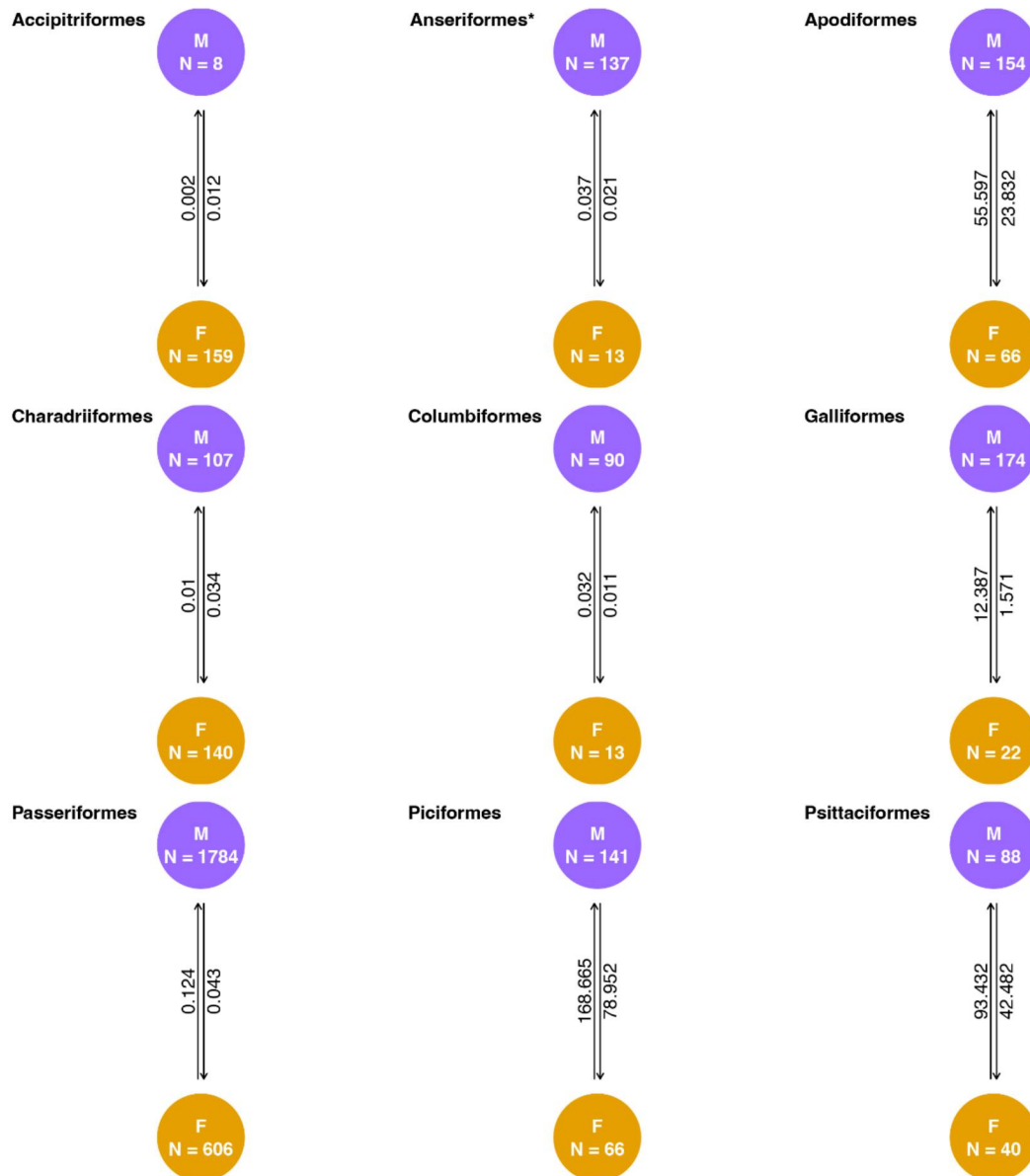
Figure 4. Transition rates between states of SSD of one topology. Purple indicates a male-biased SSD state and yellow indicating a female-biased SSD state. Inside each circle is also given the number of species in each order with that respective state. Anseriformes was the only order where forward and backward transition rates were not significantly different.

Table 2. AICw (Akaike Weights) values for the two models tested to assess the rate of transition between the types of sexual size dimorphism.

Order	N	SYM	ARD
Accipitriformes	167	0.174 (0.08-0.496)	0.826 (0.504-0.92)
Anseriformes	150	0.552 (0.355-0.691)	0.448 (0.309-0.645)

Apodiformes	247	0.218 (0-0.644)	0.782 (0.356-1)
Charadriiformes	255	0.006 (0-0.028)	0.994 (0.972-1)
Columbiformes	103	0.488 (0.304-0.604)	0.512 (0.396-0.696)
Galliformes	196	0.054 (0-0.498)	0.946 (0.502-1)
Passeriformes	2510	0 (0-0)	1 (1-1)
Piciformes	212	0.072 (0-0.57)	0.928 (0.43-1)
Psittaciformes	130	0.26 (0-0.871)	0.74 (0.129-1)

236 "SYM" corresponds to the symmetric model, where rates can vary for different transitions, but forward and
237 backward rates are the same. "ARD" corresponds to the model where all rates are different. Variation in AICw
238 values corresponds to the mean and range of values across 100 alternative topologies.
239
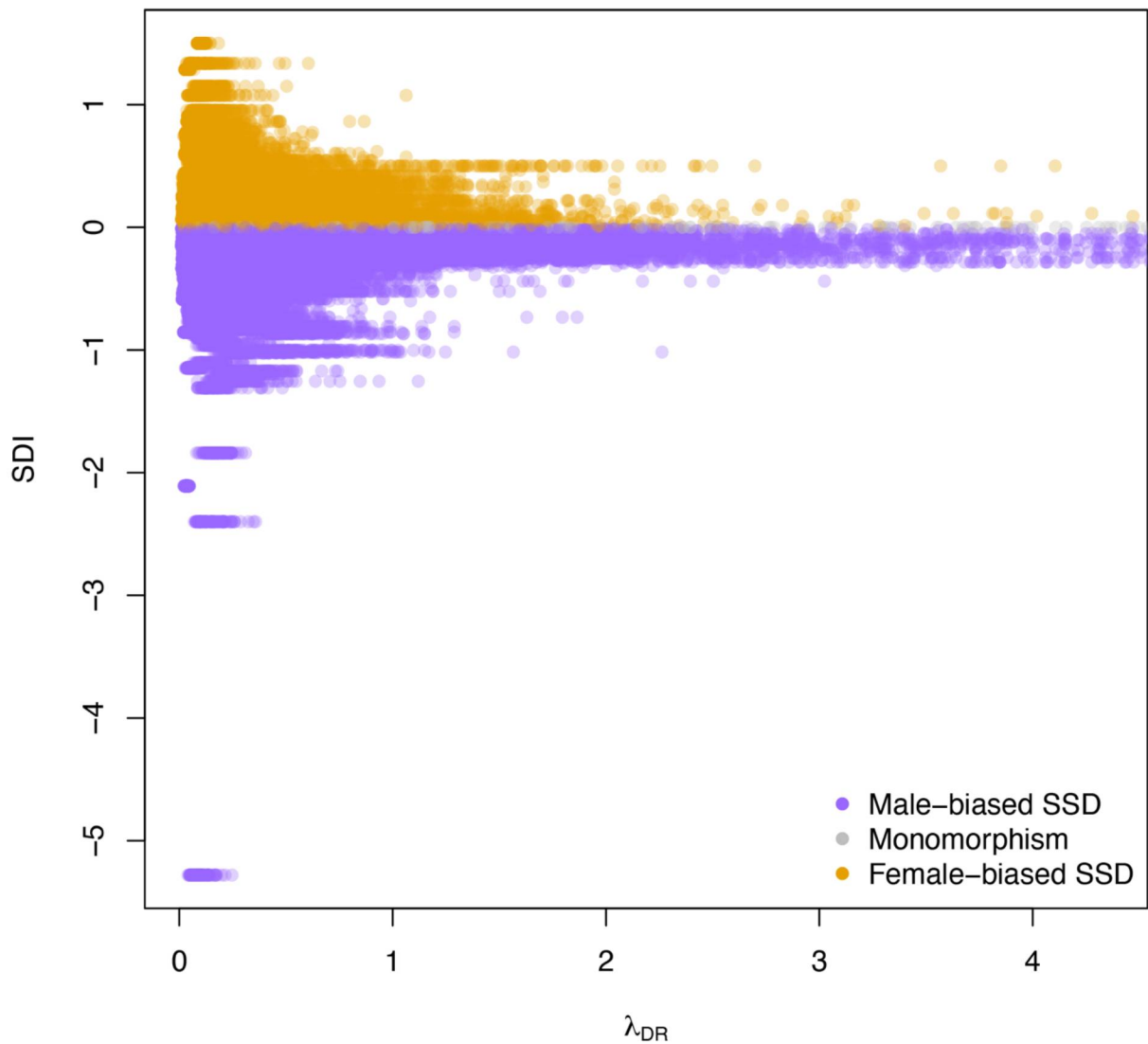
240

241 **Figure 5.** Relationship between the metric λ_{DR}, interpreted as the diversification rate, and the
242 degree of SSD. Different colors represent variations in the direction of SSD.

243

244   Comparisons between evolutionary rates of male and female body size are provided in

245   Table 3. The rate of female body mass evolution is higher than in males only for Passeriformes;

246   rates are either similar (Columbiformes, Galliformes, Piciformes, and Psittaciformes), or higher

247   in males (Accipitriformes, Anseriformes, Apodiformes, and Charadriiformes). Analyses using

248   RRphylo to auto-detect shifts in the evolutionary rate also show distinct patterns among orders

249   (Fig. 6, 7). Most shifts in the degree of SDI involve a decrease in its rate of evolution in five

250   orders, namely Accipitriformes, Anseriformes, Columbiformes, Piciformes, and Psittaciformes.

251   For another three orders, Apodiformes, Charadriiformes, and Passeriformes, most shifts

252   account for an increase in the evolutionary rate of SDI, whereas the same amount of positive

253   and negative shifts is found in Galliformes. The second analysis of RRphylo do not allow

254   detecting evidence that the rates of evolution of male or female body mass are influenced by

255   the direction of SDI (Supplementary Information, Table S1; Fig. S1, S2). Only Accipitriformes

256   has the rate of female body mass higher when species have female-biased SSD than when they

257   have male-biased SSD. Finally, PGLS analyses of species richness, absolute latitude,

258   temperature and precipitation seasonality, and NPP against SDI do not reveal any detectable

259   trends in any of the tested bird orders (Table 4; Supplementary Information, Fig. S3-S7).

260

261   **Table 3.** Rates of evolution of male and female body size calculated under a multiple-rate

262   model.

Order	N	SDI	σ^2 male body size	σ^2 female body size	p
Accipitriformes	167	Median = 0.278 (Min = -0.587; Max = 1.5)	0.057 (0.046-0.069)	0.056 (0.054-0.057)	0.001 (0-0.96)
Anseriformes	150	Median = -0.127 (Min = -1.104; Max = 0.333)	0.202 (0.09-0.315)	0.153 (0.075-0.232)	0 (0-0.817)
Apodiformes	247	Median = -0.062 (Min = -0.557; Max = 0.5)	0.02 (0.018-0.022)	0.016 (0.014-0.019)	0 (0-0.96)
Charadriiformes	255	Median = 0.017 (Min = -0.657; Max = 0.862)	0.076 (0.072-0.08)	0.07 (0.069-0.072)	0.003 (0-0.751)
Columbiformes	103	Median = -0.061 (Min = -0.613; Max = 0.183)	0.035 (0.013-0.057)	0.032 (0.013-0.05)	0.254 (0-0.977)
Galliformes	196	Median = -0.16 (Min = -5.28; Max = 0.444)	0.036 (0.035-0.037)	0.036 (0.034-0.037)	0.251 (0-0.995)

Passeriformes	2,510	Median = -0.052 (Min = -2.4; Max = 1.286)	0.038 (0.031-0.045)	0.047 (0.025-0.07)	0 (0-0.869)
Piciformes	212	Median = -0.043 (Min = -0.905; Max = 0.75)	0.03 (0.026-0.035)	0.028 (0.023-0.033)	0.092 (0-0.999)
Psittaciformes	130	Median = -0.065 (Min = -0.468; Max = 0.524)	0.028 (0.024-0.031)	0.028 (0.026-0.03)	0.2 (0-0.995)

263 The p-value indicates the results from the likelihood ratio test between a multiple-rate model and a single-rate

264 model. SDI values account for variation between species within each taxon, whereas variation in evolutionary

265 rates and p-value correspond to the median and range of values across 100 alternative topologies.

266
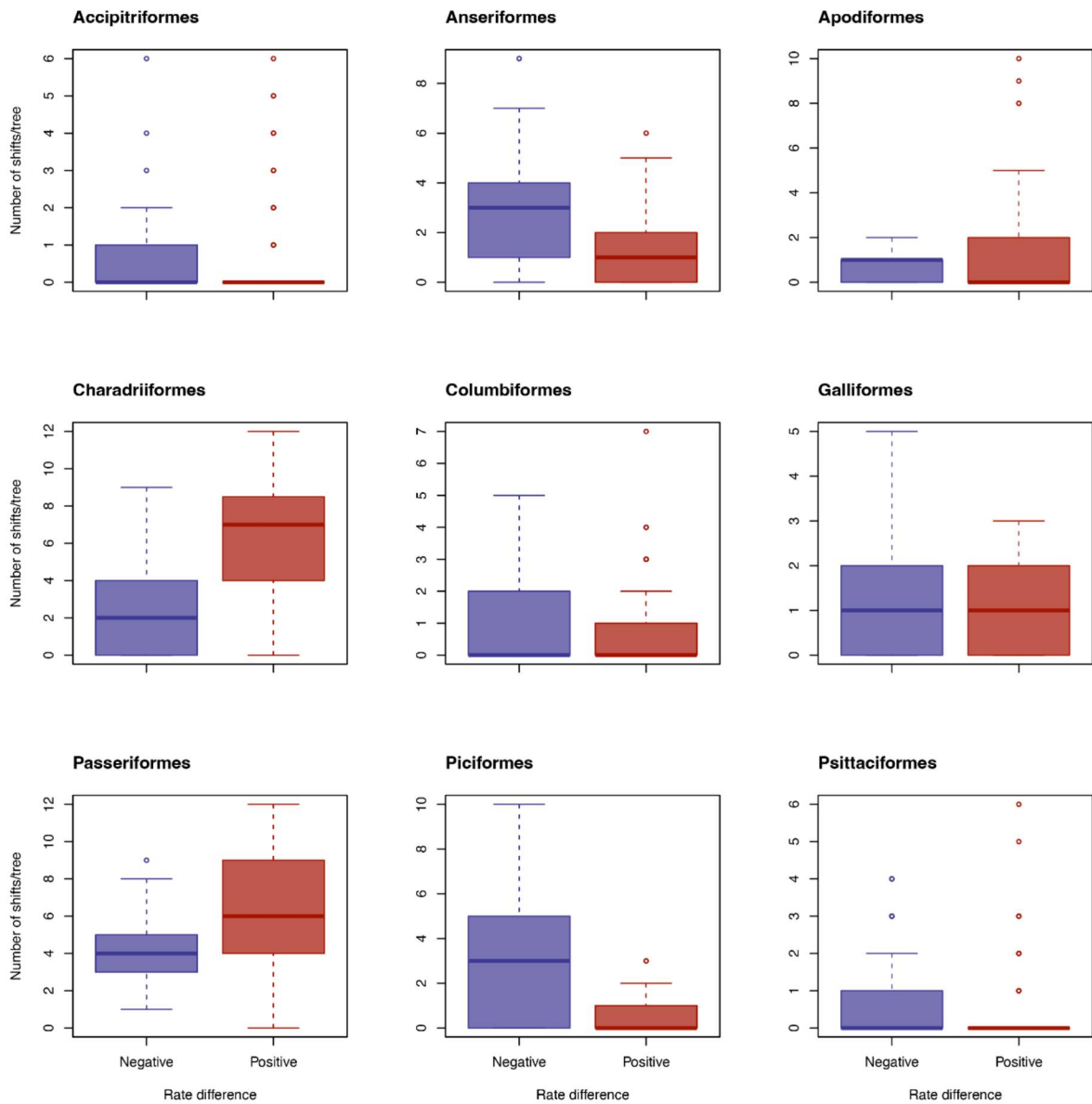
267

268 **Figure 6.** Boxplots representing the number of shifts in SSD evolutionary rate per tree across
269 100 alternative topologies. Negative shifts (i.e., decreases in evolutionary rate) are indicated in
270 blue, while positive shifts (i.e., increases in evolutionary rate) are noted in red.
271
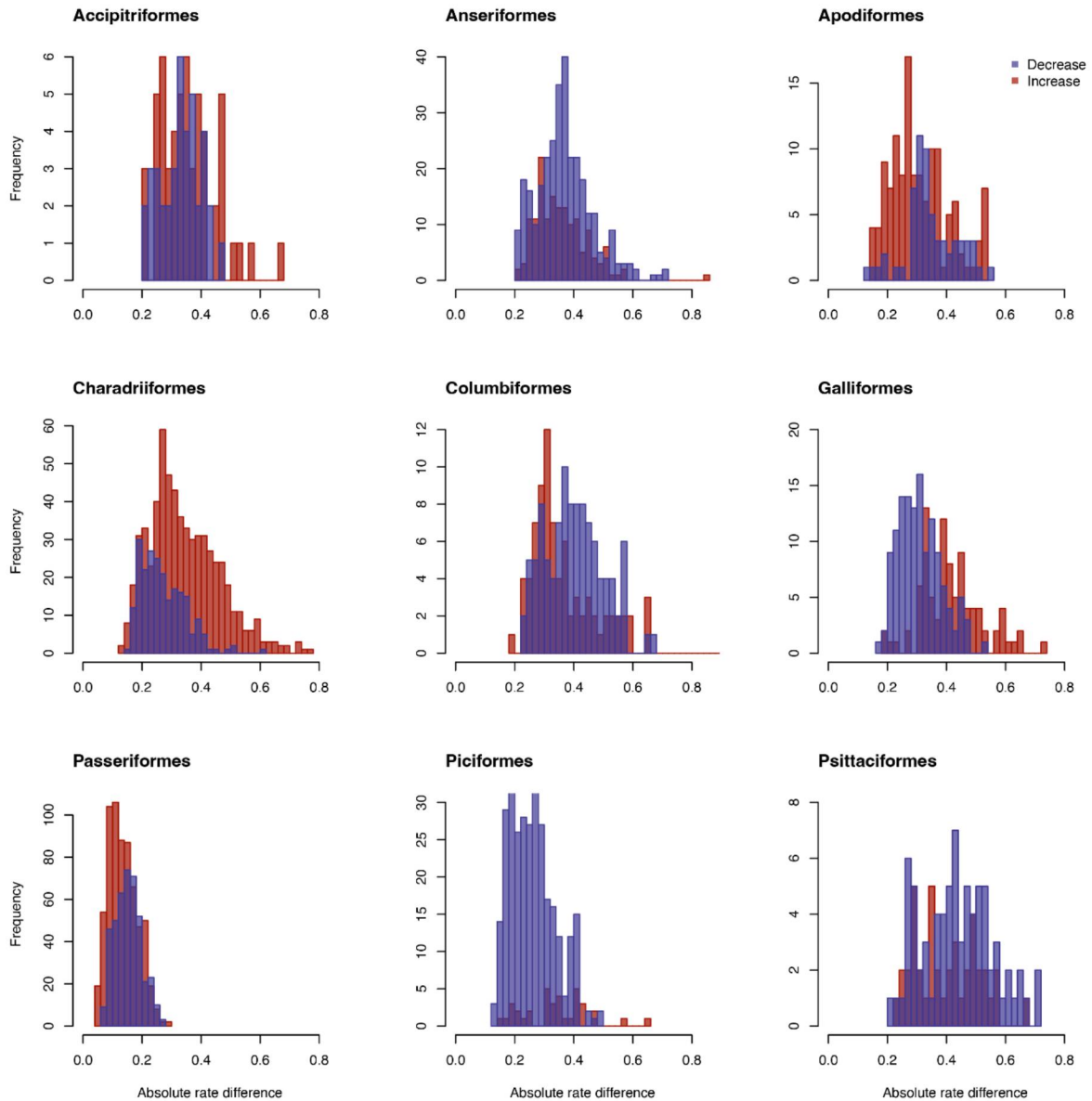
272
273 **Figure 7.** Frequency histograms representing the magnitude of the shifts estimated in SSD
274 evolutionary rate. Negative shifts (i.e., decreases in evolutionary rate) are indicated in blue,
275 while positive shifts (i.e., increases in evolutionary rate) are noted in red.
276

277 **Table 4.** Phylogenetic generalized least squared (PGLS) analyses of the relationship between SDI and order richness, absolute latitude, temperature

278 and precipitation seasonality, and net primary productivity of different bird orders.

Order	N	Order richness		Absolute latitude		Temperature seasonality		Precipitation seasonality		Net primary productivity		R^2
		Slope	p	Slope	p	Slope	p	Slope	p	Slope	p	
Accipitriformes	157	0.003 (-0.025-0.047)	0.24 (0-0.999)	0.002 (-0.035-0.019)	0.362 (0-1)	0 (0-0)	0.276 (0-0.998)	-0.001 (-0.026-0.009)	0.305 (0-0.996)	0 (-0.006-0.003)	0.216 (0-0.999)	0.174 (0.006-0.985)
Anseriformes	127	0.004 (-0.024-0.028)	0.242 (0-0.998)	0.001 (-0.023-0.038)	0.369 (0-0.999)	0 (0-0)	0.435 (0-1)	0 (-0.005-0.021)	0.341 (0-1)	0 (-0.001-0.004)	0.344 (0-0.997)	0.305 (0.012-0.992)
Apodiformes	228	-0.002 (-0.018-0.009)	0.297 (0-0.994)	-0.003 (-0.027-0.01)	0.333 (0-0.999)	0 (0-0)	0.393 (0-0.997)	0 (-0.007-0.006)	0.385 (0-0.996)	0 (-0.001-0.003)	0.188 (0-0.999)	0.115 (0.002-0.959)
Charadriiformes	234	0.002 (-0.01-0.015)	0.238 (0-0.998)	0 (-0.005-0.001)	0.662 (0-0.999)	0 (0-0)	0.348 (0-0.998)	-0.001 (-0.013-0.003)	0.165 (0-0.987)	0 (-0.003-0.001)	0.282 (0-1)	0.157 (0.008-0.971)
Columbiformes	93	-0.003 (-0.021-0.076)	0.256 (0-0.999)	0.002 (-0.029-0.012)	0.263 (0-1)	0 (0-0)	0.505 (0-0.999)	0 (-0.007-0.005)	0.343 (0-0.999)	0 (-0.001-0.003)	0.473 (0-0.999)	0.259 (0.027-0.998)
Galliformes	164	-0.009 (-0.202-0.078)	0.354 (0-0.994)	0.006 (-0.023-0.155)	0.42 (0-0.998)	0 (0-0)	0.632 (0-0.999)	0.002 (-0.004-0.048)	0.262 (0-1)	0 (-0.003-0.017)	0.477 (0-1)	0.097 (0.003-0.764)
Passeriformes	1,999	0 (-0.004-0.003)	0.165 (0-0.979)	0 (-0.022-0.013)	0.156 (0-0.998)	0 (0-0)	0.18 (0-0.998)	0 (-0.003-0.004)	0.133 (0-0.999)	0 (-0.002-0.002)	0.147 (0-0.984)	0.11 (0.001-0.988)
Piciformes	177	0.001 (-0.036-0.063)	0.296 (0-0.998)	0 (-0.089-0.047)	0.457 (0-0.999)	0 (0-0)	0.428 (0-0.995)	0 (-0.019-0.007)	0.326 (0-1)	0 (-0.004-0.003)	0.227 (0-0.999)	0.134 (0.003-0.976)

| Psittaciformes | 115 | 0.005 (-0.01-0.037) | 0.092 (0-0.971) | -0.001 (-0.01-0.01) | 0.429 (0-0.999) | 0 (0-0) | 0.458 (0-0.998) | 0 (-0.005-0.009) | 0.464 (0-0.999) | 0 (-0.002-0.003) | 0.272 (0-0.996) | 0.177 (0.051-0.96) |

Estimates are given as mean values and the range of values across 1000 alternative topologies.

281   4.   Discussion

282   In this study, we explore a large-scale dataset on body size across different avian
283   lineages to test four alternative hypotheses on the evolution of sexual size dimorphism, namely
284   the sexual selection, fecundity, niche divergence, and allometry hypotheses (Table 1). There
285   was no clear support for a single mechanism, and the level of support for different hypotheses
286   varied across avian orders. Taxa in which female-biased SSD is more prevalent (i.e.,
287   Accipitriformes and Charadriiformes) tended to favour both the fecundity (higher transition
288   rates to female-biased SSD) and sexual selection (higher evolutionary rate for male size)
289   hypotheses. On the other hand, taxa in which male-biased SSD were most common were more
290   varied in their favoured hypotheses. In Passeriformes, fecundity selection and sexual selection
291   hypotheses were also supported, but with the reverse order of the corresponding tests in relation
292   to Accipitriformes and Charadriiformes (i.e., higher evolutionary rate for female size and higher
293   transition rate to male- SSD, respectively). Likewise, niche divergence (equal transition rates
294   between different kinds of SSD) and sexual selection (a higher rate of evolution for male size)
295   were supported for Anseriformes, but reverse order of the corresponding tests for
296   Columbiformes, Galliformes, Piciformes, and Psittaciformes (higher transition rates to male-
297   biased SSD and similar evolutionary rates for males and females). The allometry hypothesis
298   was supported in Anseriformes and Apodiformes, as evidenced by higher evolutionary rates in
299   male body size and a predominantly male-biased SSD. Finally, we found no evidence that the
300   direction of SSD (i.e., if male- or female biased) affected the rate of evolution of male or female
301   body size, except for female size in Accipitriformes (Supplementary Information, Table S1;
302   Fig. S2). These results suggest that, although the allometry hypothesis received limited support,
303   all remaining three hypotheses seem to be supported, to different degrees, in each avian order.

304   We did not find any evidence of a direct association between environmental factors—
305   seasonality, productivity, richness, or latitude—and the degree of SSD (Table 4; Supplementary
306   Information, Fig. S3-S7). Two previous studies explored the relationship between SSD and
307   latitude. Friedman & Remeš (2016) found substantial spatial heterogeneity in bird SSD, but no
308   association between SSD and latitude. One possible explanation for these results could be that
309   the effect of productivity might be apparent only at lower trophic levels, as in the case of
310   herbivores (Henry *et al.*, 2023), and therefore might not affect the higher trophic levels
311   characteristic of most avian lineages in our analyses. However, Tarr et al. (2019) showed that
312   lizards from Central and North America tend to have more male-biased SSD at low latitudes,
313   but female-biased SSD is more common at higher latitudes. This discrepancy might suggest

314 that the effects of environmental factors on SSD might be scale-dependent, and might not be as
315 apparent at the large spatial scales involved in our study.

316 The lack of clear environmental correlates of SSD is intriguing, given the spatial
317 patterns detected when mapping variation of SSD (Fig. 3). For instance, high latitudes are often
318 characterised by extreme SSD of both sexes, with female-biased SSD being widespread in
319 North America and parts of Europe, whereas male-biased SSD is more common in Africa.
320 Previous studies showed inconsistent support for geographical patterns of SSD. Using display
321 agility as a proxy for sexual selection, Serrano-Meneses & Székely (2006) found support for
322 sexual selection predicting SSD in seabirds but did not find support for fecundity selection or
323 niche partitioning. Similar results were found by Lislevand et al. (2009) for Phasianidae, as did
324 Nuñez-Rosas et al. (2017) for hummingbirds, using lekking behaviour as a proxy for sexual
325 selection. Pérez-Camacho et al. (2018), however, found ecological correlates to predict female-
326 biased SSDs in diurnal raptors. Our study explored these hypotheses using a macroevolutionary
327 approach and also found different levels of support for each hypothesis, suggesting that the
328 mechanisms driving SSD are not only multifactorial but also that the most important
329 mechanisms might change in different avian lineages.

330 There are several caveats that should be noted in our study. Firstly, we focused on SSD,
331 which is only one of the dimensions of sexual dimorphism. It is important to acknowledge that
332 alternative dimensions of the dimorphism do not necessarily evolve in parallel with SSD
333 (Figuerola & Green, 2000; Gonzalez-Voyer et al., 2022). Body size is a major component of
334 the life history of an organism, influencing several other physiological and ecological aspects,
335 and is certainly one of the main components of sexual dimorphism (Fairbairn, 2016). However,
336 one might expect that, for instance, plumage dimorphism might already alleviate the need for
337 SSD in the context of sexual selection, yet the exploration of potential trade-offs between
338 different dimensions of sexual dimorphism is still in their infancy, particularly in
339 macroevolutionary studies (but see Gonzalez-Voyer et al., 2022). Secondly, other variables are
340 thought to influence the degree of sexual dimorphism, such as parental care (Horne et al., 2020)
341 and mating systems (Nuñez-Rosas et al., 2017). However, it is worth noting that some of these
342 traits are indirectly encompassed within the hypotheses we tested, such as parental care and
343 mating systems stemming from the sexual selection hypothesis for larger males (Webster, 1992;
344 Dale et al., 2007; Gonzalez-Voyer et al., 2022). Additionally, it is important to consider the
345 potential influence of the agility display hypothesis when interpreting the results of the sexual
346 selection hypothesis. According to this scenario, smaller sizes would be advantageous for
347 species that rely on aerial displays to attract females (Jehl & Murray, 1986). Our findings

348 suggest that Accipitriformes and Charadriiformes may provide support for this hypothesis, as
349 they exhibit higher transition rates towards female-biased sexual size dimorphism (i.e., smaller
350 males) and greater evolutionary rates for male body mass.

351 In this study, we demonstrate that SSD evolution is likely to be multifactorial, with
352 sexual selection, fecundity, and niche divergence playing important roles in different avian
353 orders. On the other hand, purely environmental factors, such as temperature seasonality and
354 productivity, seem poor predictors of SSD. Further studies, particularly at smaller spatial and
355 temporal scales, can be useful to understand those differences across taxa. Finally, our study
356 underscores the usefulness of an explicitly macroevolutionary approach to understand drivers
357 of SSD.

358

363

364 **6.   CRediT Statement**

365 Fernanda S. Caron (conceptualization, data curation, formal analysis, funding
366 acquisition, investigation, methodology, project administration, resources, software, validation,
367 visualization, writing – original draft, writing – review & editing) and Marcio R. Pie
368 (conceptualization, project administration, resources, supervision, writing – review & editing).

369

370 **7.   Competing Interests Statement**

371 The authors declare no competing interests.

372

373 **8.   Data Availability Statement**

374 All data used in our analyses is available in Supplementary Information, Table S2. Codes
375 used in our study are available at https://github.com/fernandacaron/dimorphism_evol.

376

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501

502 **10.   Supplementary Information**

503 **Table S1.** p value of the difference between the average absolute rate residuals of different
504 regimes or between the regime and the rest of the tree.

505 **Table S2.** Male and female body size data used in the analyses.

506 **Figure S1.** Density distributions of absolute male body mass (g) rate residuals.

507 **Figure S2.** Density distributions of absolute female body mass (g) rate residuals.

508 **Figure S3.** Relationship between the order richness and the degree of SSD.

509   **Figure S4**. Relationship between the absolute latitude and the degree of SSD.

510   **Figure S5.** Relationship between temperature seasonality and the degree of SSD.

511   **Figure S6**. Relationship between precipitation seasonality and the degree of SSD.

512   **Figure S7**. Relationship between net primary productivity and the degree of SSD.

513

514   **Tables**

515

516   Table 1. Predictions of the four hypotheses tested in the present study as potential drivers of SSD. See text for

517   details.

Hypothesis	Transitions between types of SSD	Rates of body mass evolution	Spatial/ecological correlates
Sexual selection	♂ SSD → ♀ SSD < ♀ SSD → ♂ SSD	Rate of ♂ > Rate of ♀	No clear prediction
Fecundity	♂ SSD → ♀ SSD > ♀ SSD → ♂ SSD	Rate of ♂ < Rate of ♀	Positive relationship between ♀ SSD and seasonality
Niche divergence	♂ SSD → ♀ SSD ≈ ♀ SSD → ♂ SSD	Rate of ♂ ≈ Rate of ♀	Positive relationship between absolute SSD and species richness + productivity
Allometry	No clear prediction	Rate of body size evolution should be faster in the larger sex	Positive relationship between absolute SSD and latitude

518

519 **Table 2.** AICw (Akaike Weights) values for the two models tested to assess the rate of transition between the types
520 of sexual size dimorphism.

Order	N	SYM	ARD
Accipitriformes	167	0.174 (0.08-0.496)	0.826 (0.504-0.92)
Anseriformes	150	0.552 (0.355-0.691)	0.448 (0.309-0.645)
Apodiformes	247	0.218 (0-0.644)	0.782 (0.356-1)
Charadriiformes	255	0.006 (0-0.028)	0.994 (0.972-1)
Columbiformes	103	0.488 (0.304-0.604)	0.512 (0.396-0.696)
Galliformes	196	0.054 (0-0.498)	0.946 (0.502-1)
Passeriformes	2510	0 (0-0)	1 (1-1)
Piciformes	212	0.072 (0-0.57)	0.928 (0.43-1)
Psittaciformes	130	0.26 (0-0.871)	0.74 (0.129-1)

521 "SYM" corresponds to the symmetric model, where rates can vary for different transitions, but forward and
522 backward rates are the same. "ARD" corresponds to the model where all rates are different. Variation in AICw
523 values corresponds to the mean and range of values across 100 alternative topologies.
524

525 **Table 3.** Rates of evolution of male and female body size calculated under a multiple-rate model.

Order	N	SDI	σ^2 male body size	σ^2 female body size	p
Accipitriformes	167	Median = 0.278 (Min = -0.587; Max = 1.5)	0.057 (0.046-0.069)	0.056 (0.054-0.057)	0.001 (0-0.96)
Anseriformes	150	Median = -0.127 (Min = -1.104; Max = 0.333)	0.202 (0.09-0.315)	0.153 (0.075-0.232)	0 (0-0.817)
Apodiformes	247	Median = -0.062 (Min = -0.557; Max = 0.5)	0.02 (0.018-0.022)	0.016 (0.014-0.019)	0 (0-0.96)
Charadriiformes	255	Median = 0.017 (Min = -0.657; Max = 0.862)	0.076 (0.072-0.08)	0.07 (0.069-0.072)	0.003 (0-0.751)
Columbiformes	103	Median = -0.061 (Min = -0.613; Max = 0.183)	0.035 (0.013-0.057)	0.032 (0.013-0.05)	0.254 (0-0.977)
Galliformes	196	Median = -0.16 (Min = -5.28; Max = 0.444)	0.036 (0.035-0.037)	0.036 (0.034-0.037)	0.251 (0-0.995)
Passeriformes	2,510	Median = -0.052 (Min = -2.4; Max = 1.286)	0.038 (0.031-0.045)	0.047 (0.025-0.07)	0 (0-0.869)
Piciformes	212	Median = -0.043 (Min = -0.905; Max = 0.75)	0.03 (0.026-0.035)	0.028 (0.023-0.033)	0.092 (0-0.999)
Psittaciformes	130	Median = -0.065 (Min = -0.468; Max = 0.524)	0.028 (0.024-0.031)	0.028 (0.026-0.03)	0.2 (0-0.995)

526 The p-value indicates the results from the likelihood ratio test between a multiple-rate model and a single-rate
527 model. SDI values account for variation between species within each taxon, whereas variation in evolutionary
528 rates and p-value correspond to the median and range of values across 100 alternative topologies.

529

Table 4. Phylogenetic generalized least squared (PGLS) analyses of the relationship between order richness, absolute latitude, temperature and precipitation seasonality, and net primary productivity of different bird orders.

Order	N	Order richness		Absolute latitude		Temperature seasonality		Precipitation seasonality		Net primary productivity		R^2
		Slope	p	Slope	p	Slope	p	Slope	p	Slope	p	
Accipitriformes	157	0.003 (-0.025-0.047)	0.24 (0-0.999)	0.002 (-0.035-0.019)	0.362 (0-1)	0 (0-0)	0.276 (0-0.998)	-0.001 (-0.026-0.009)	0.305 (0-0.996)	0 (-0.006-0.003)	0.216 (0-0.999)	0.174 (0.006-0.985)
Anseriformes	127	0.004 (-0.024-0.028)	0.242 (0-0.998)	0.001 (-0.023-0.038)	0.369 (0-0.999)	0 (0-0)	0.435 (0-1)	0 (-0.005-0.021)	0.341 (0-1)	0 (-0.001-0.004)	0.344 (0-0.997)	0.305 (0.012-0.992)
Apodiformes	228	-0.002 (-0.018-0.009)	0.297 (0-0.994)	-0.003 (-0.027-0.01)	0.333 (0-0.999)	0 (0-0)	0.393 (0-0.997)	0 (-0.007-0.006)	0.385 (0-0.996)	0 (-0.001-0.003)	0.188 (0-0.999)	0.115 (0.002-0.959)
Charadriiformes	234	0.002 (-0.01-0.015)	0.238 (0-0.998)	0 (-0.005-0.001)	0.662 (0-0.999)	0 (0-0)	0.348 (0-0.998)	-0.001 (-0.013-0.003)	0.165 (0-0.987)	0 (-0.003-0.001)	0.282 (0-1)	0.157 (0.008-0.971)
Columbiformes	93	-0.003 (-0.021-0.076)	0.256 (0-0.999)	0.002 (-0.029-0.012)	0.263 (0-1)	0 (0-0)	0.505 (0-0.999)	0 (-0.007-0.005)	0.343 (0-0.999)	0 (-0.001-0.003)	0.473 (0-0.999)	0.259 (0.027-0.998)
Galliformes	164	-0.009 (-0.202-0.078)	0.354 (0-0.994)	0.006 (-0.023-0.155)	0.42 (0-0.998)	0 (0-0)	0.632 (0-0.999)	0.002 (-0.004-0.048)	0.262 (0-1)	0 (-0.003-0.017)	0.477 (0-1)	0.097 (0.003-0.764)
Passeriformes	1,999	0 (-0.004-0.003)	0.165 (0-0.979)	0 (-0.022-0.013)	0.156 (0-0.998)	0 (0-0)	0.18 (0-0.998)	0 (-0.003-0.004)	0.133 (0-0.999)	0 (-0.002-0.002)	0.147 (0-0.984)	0.11 (0.001-0.988)
Piciformes	177	0.001 (-0.036-0.063)	0.296 (0-0.998)	0 (-0.089-0.047)	0.457 (0-0.999)	0 (0-0)	0.428 (0-0.995)	0 (-0.019-0.007)	0.326 (0-1)	0 (-0.004-0.003)	0.227 (0-0.999)	0.134 (0.003-0.976)

		0.005 (-0.01-0.037)	0.092 (0-0.971)	-0.001 (-0.01-0.01)	0.429 (0-0.999)	0 (0-0)	0.458 (0-0.998)	0 (-0.005-0.009)	0.464 (0-0.999)	0 (-0.002-0.003)	0.272 (0-0.996)	0.177 (0.051-0.96)
Psittaciformes	115											

532 Estimates are given as mean values and the range of values across 1000 alternative topologies.

533

534   **Figure captions**

535

536   **Figure 1.** Frequency distributions of body mass (g) across the nine studied orders. Within each

537   order, different colours represent the distribution of each sex. Values were ln-transformed prior

538   to visualization.

539

540   **Figure 2.** Stochastic character mapping of sexual size dimorphism coded as male-biased,

541   female-biased, or monomorphic. Bars at the top of the phylogeny tips correspond to log body

542   mass (g) of each species, calculated as the average of the male and female body mass. As shown

543   in Fig. 1, the nine orders selected for the present study are represented by arcs with their

544   respective silhouettes.

545

546   **Figure 3.** Geographic distribution of avian sexual size dimorphism. SSD was measured by the

547   index of Lovich & Gibbons (1992). A. Median value across all species found on each cell; B.

548   median values considering only species with male-biased sexual size dimorphism (SSD); C.

549   median values considering only species with female-biased SSD.

550

551   **Figure 4**. Transition rates between states of SSD of one topology. Purple indicates a male-

552   biased SSD state and yellow indicating a female-biased SSD state. Inside each circle is also

553   given the number of species in each order with that respective state. Anseriformes was the only

554   order where forward and backward transition rates were not significantly different.

555

556   **Figure 5.** Relationship between the metric λ_{DR}, interpreted as the diversification rate, and the

557   degree of SSD. Different colors represent variations in the direction of SSD.

558

559   **Figure 6.** Boxplots representing the number of shifts in SSD evolutionary rate per tree across

560   100 alternative topologies. Negative shifts (i.e., decreases in evolutionary rate) are indicated in

561   blue, while positive shifts (i.e., increases in evolutionary rate) are noted in red.

562

563   **Figure 7.** Frequency histograms representing the magnitude of the shifts estimated in SSD

564   evolutionary rate. Negative shifts (i.e., decreases in evolutionary rate) are indicated in blue,

565   while positive shifts (i.e., increases in evolutionary rate) are noted in red.

566

567   **Supporting Information**

568

569   **The macroevolution of sexual size dimorphism in birds**

570

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572

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576

577   **Table S1.** p value of the difference between the average absolute rate residuals of different

578   regimes or between the regime and the rest of the tree.

579

580   **Figure S1.** Density distributions of absolute male body mass (g) rate residuals.

581

582   **Figure S2.** Density distributions of absolute female body mass (g) rate residuals.

583

584   **Figure S3.** Relationship between the order richness and the degree of SSD.

585

586   **Figure S4.** Relationship between the absolute latitude and the degree of SSD.

587

588   **Figure S5.** Relationship between temperature seasonality and the degree of SSD.

589

590   **Figure S6.** Relationship between precipitation seasonality and the degree of SSD.
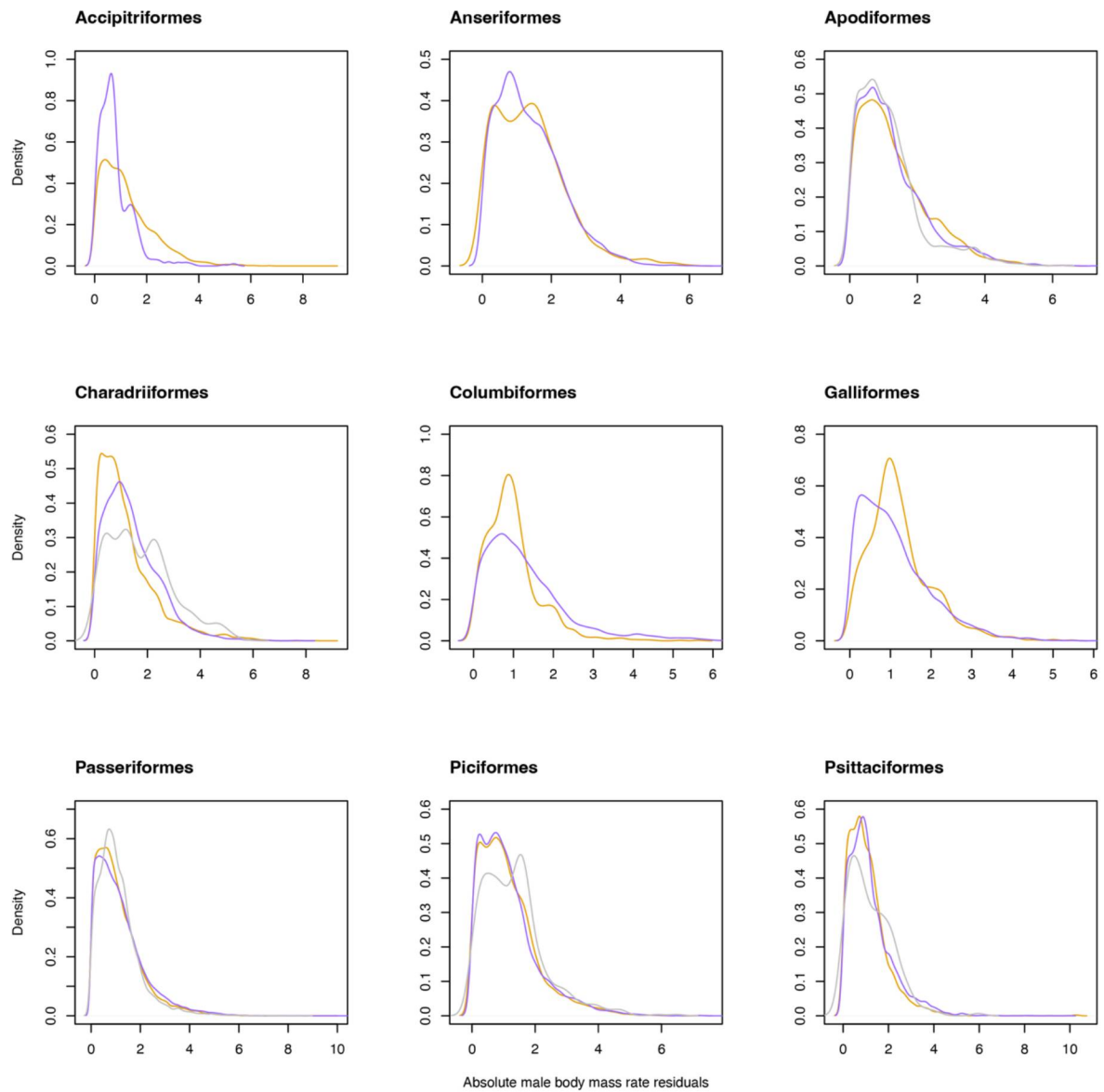
591

592   **Figure S7.** Relationship between net primary productivity and the degree of SSD.

593

594 **Table S1.** p value of the difference between the average absolute rate residuals of different regimes or between the regime and the rest of the tree. Body mass for male and
595 female evolution are compare for each regime state, that is, when the species have female-biased SSD, male-biased SSD or when it is monomorphic. Values correspond to the
596 median and range of values across 100 alternative topologies.

Character states		Order								
		Accipitriformes	**Anseriformes**	**Apodiformes**	**Charadriiformes**	**Columbiformes**	**Galliformes**	**Passeriformes**	**Piciformes**	**Psittaciformes**
ale body mass (g)	Male-biased SSD - Female-biased SSD	0.087 (0.003-0.624)	0.456 (0.022-0.974)	0.328 (0.021-0.974)	0.919 (0.421-0.999)	0.866 (0.39-0.994)	0.27 (0.004-0.939)	0.966 (0.327-1)	0.533 (0.023-0.997)	0.802 (0.003-0.999)
	Monomorphism - Female-biased SSD	NA	NA	0.213 (0.002-0.938)	0.892 (0.187-0.996)		NA	NA	0.455 (0.011-0.893)	0.683 (0.008-0.977)	0.579 (0.029-0.978)
	Monomorphism - Male-biased SSD	NA	NA	0.279 (0.015-0.953)	0.811 (0.174-0.991)		NA	NA	0.132 (0.002-0.795)	0.662 (0.039-0.982)	0.57 (0.01-0.984)
	Female-biased SSD	NA	NA	0.616 (0.035-0.986)	0.21 (0.001-0.993)		NA	NA	0.045 (0.001-0.709)	0.567 (0.005-0.976)	0.772 (0.003-0.994)
	Monomorphism	NA	NA	0.308 (0.013-0.995)	0.688 (0.001-0.992)		NA	NA	0.966 (0.11-1)	0.383 (0.008-0.995)	0.214 (0.001-0.997)
	Male-biased SSD	NA	NA	0.47 (0.012-0.99)	0.859 (0.01-0.995)		NA	NA	0.235 (0.002-1)	0.666 (0.02-0.981)	0.569 (0.017-0.982)
emale body mass (g)	Male-biased SSD - Female-biased SSD	**0.002 (0.001-0.231)**	0.469 (0.008-0.926)	0.131 (0.002-0.89)	0.95 (0.535-1)	0.954 (0.588-1)	0.809 (0.1-0.987)	0.966 (0.434-1)	0.476 (0.014-0.982)	0.908 (0.061-1)
	Monomorphism - Female-biased SSD	NA	NA	0.188 (0.002-0.824)	0.946 (0.463-0.998)		NA	NA	0.384 (0.028-0.943)	0.675 (0.04-0.997)	0.665 (0.02-0.998)
	Monomorphism - Male-biased SSD	NA	NA	0.386 (0.046-0.988)	0.852 (0.317-0.994)		NA	NA	0.116 (0.001-0.902)	0.702 (0.075-0.999)	0.545 (0.012-0.994)
	Female-biased SSD	NA	NA	0.816 (0.034-0.997)	0.142 (0.001-0.996)		NA	NA	0.056 (0.001-0.649)	0.552 (0.032-0.983)	0.891 (0.091-0.999)

Monomorphism	NA	NA	0.422 (0.012-1)	0.764 (0.001-0.999)	NA	NA	0.968 (0.015-1)	0.366 (0.002-0.982)	0.096 (0.001-0.953)
Male-biased SSD	NA	NA	0.226 (0.004-0.837)	0.92 5-0.997)	NA	NA	0.182 (0.002-1)	0.678 (0.065-0.999)	0.584 (0.03-0.996)

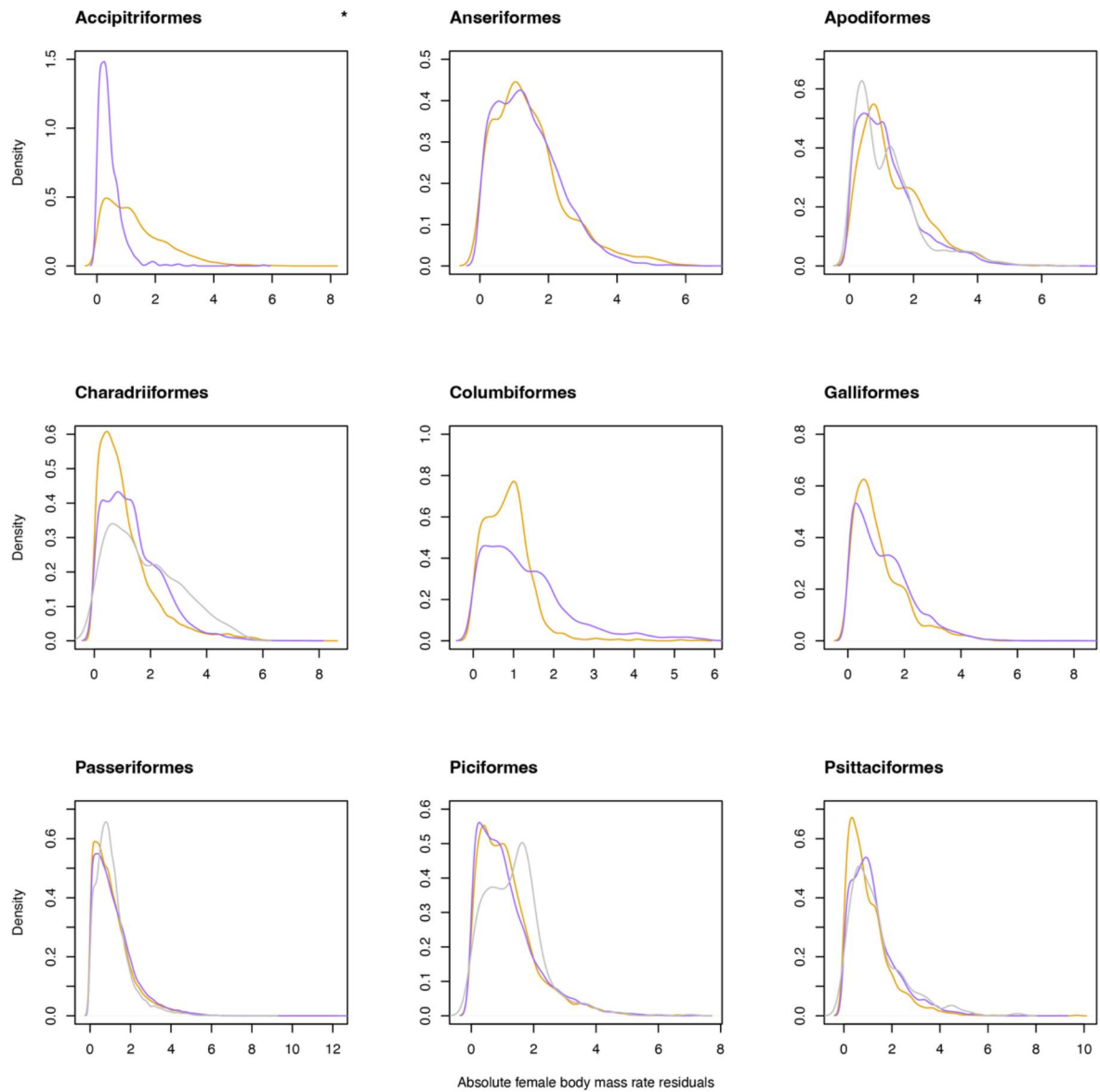597

Figure S1. Density distributions of absolute male body mass (g) rate residuals. Different distributions correspond to the assessment of male body mass evolution when the species presented one of the three SSD states: male-biased (purple), female-biased (yellow), or monomorphism (gray).

Figure S2. Density distributions of absolute female body mass (g) rate residuals. Different distributions correspond to the assessment of female body mass evolution when the species presented one of the three SSD states: male-biased (purple), female-biased (yellow), or monomorphism (gray).
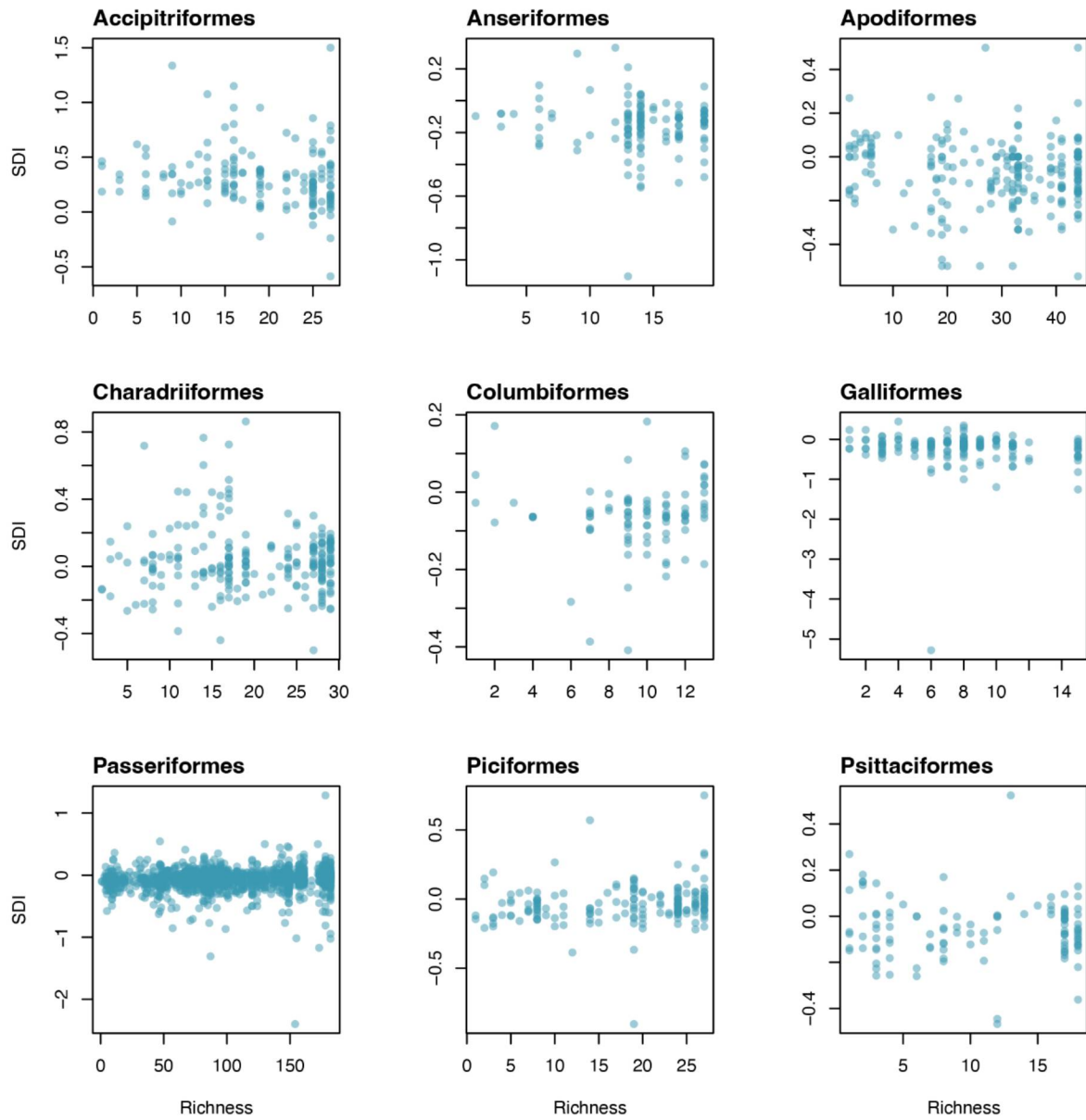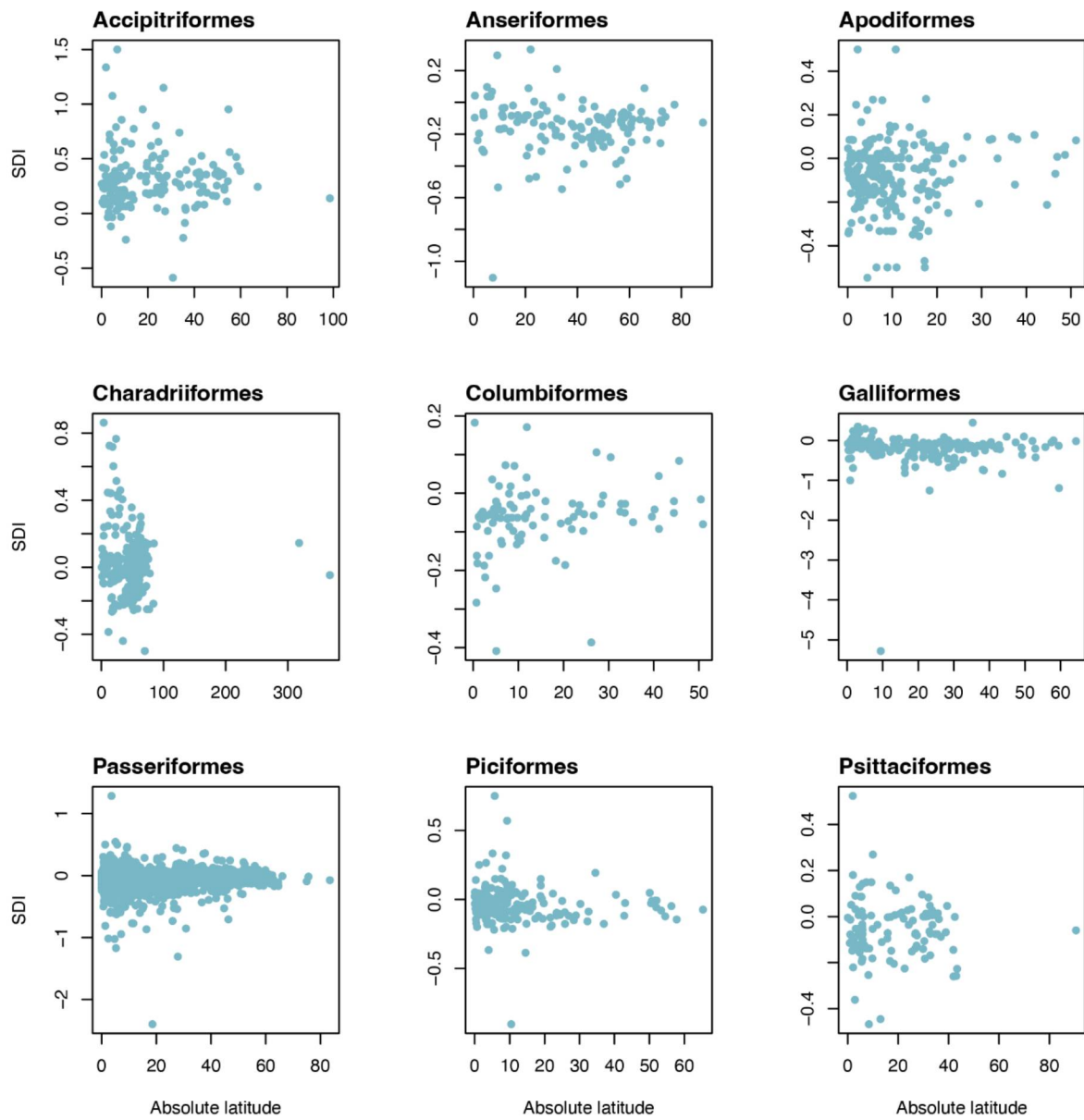
608

609 **Figure S3**. Relationship between the order richness and the degree of SSD.

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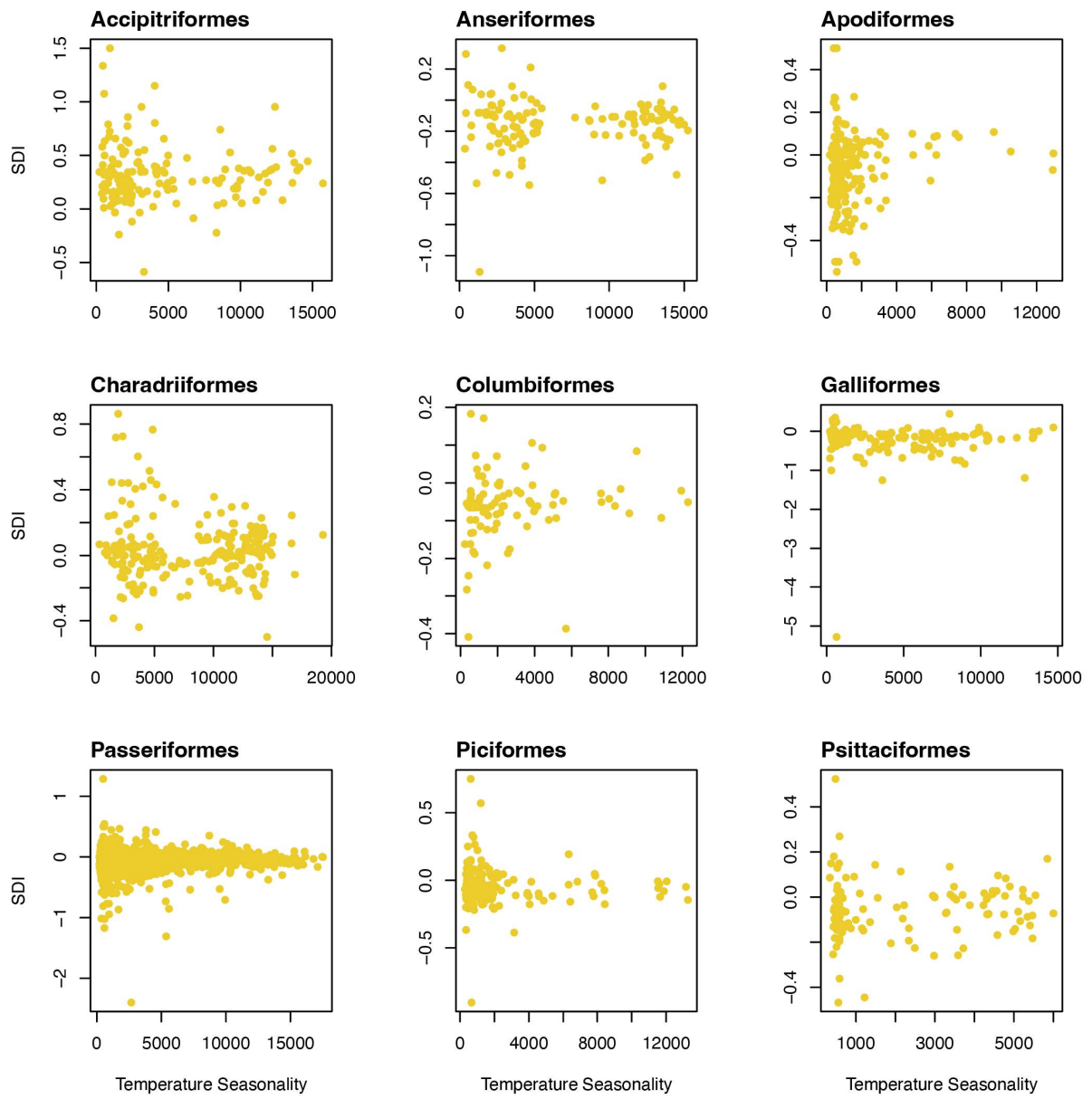**Figure** S4. Relationship between the absolute latitude and the degree of SSD.

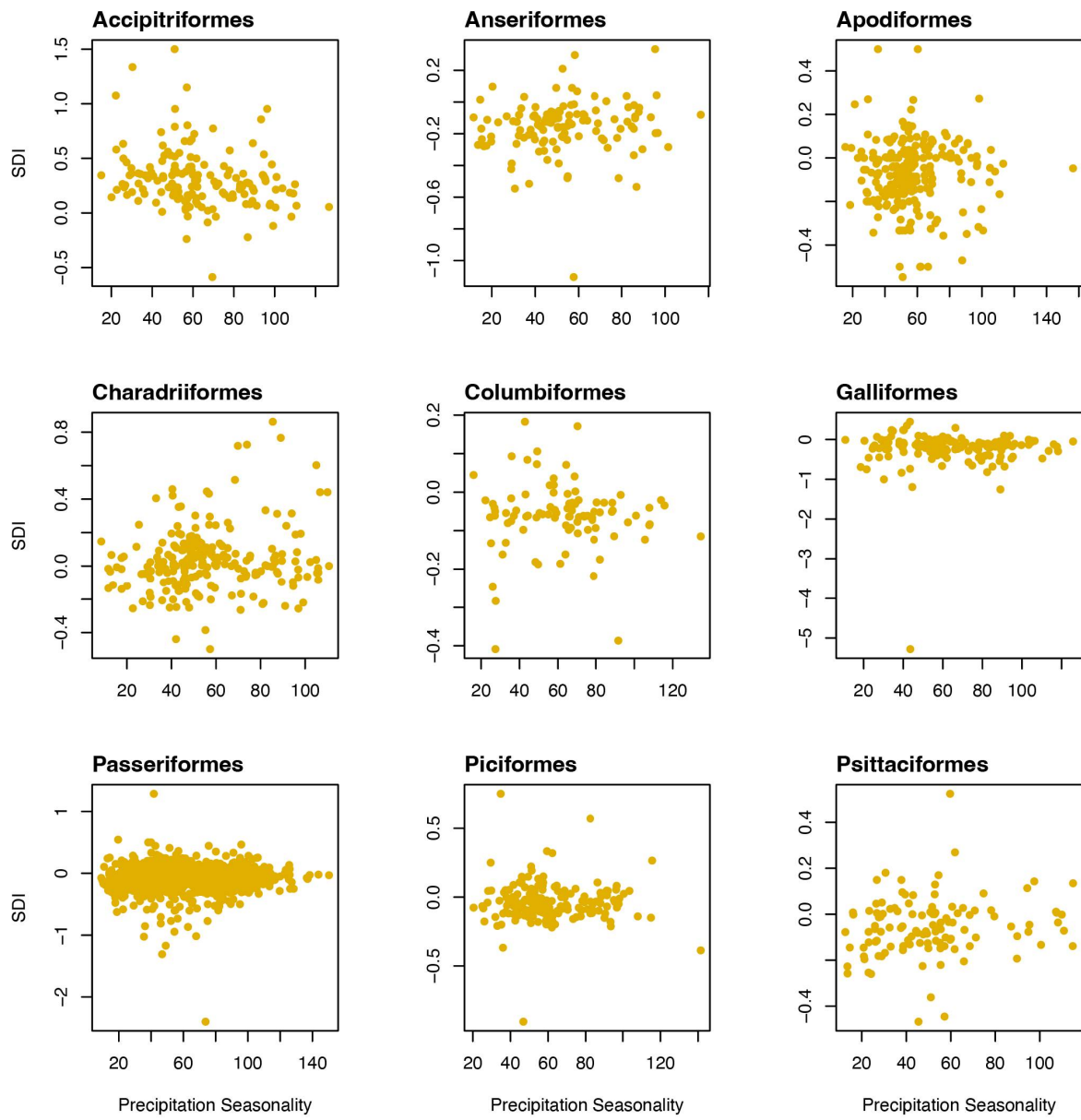**Figure S5**. Relationship between temperature seasonality and the degree of SSD.

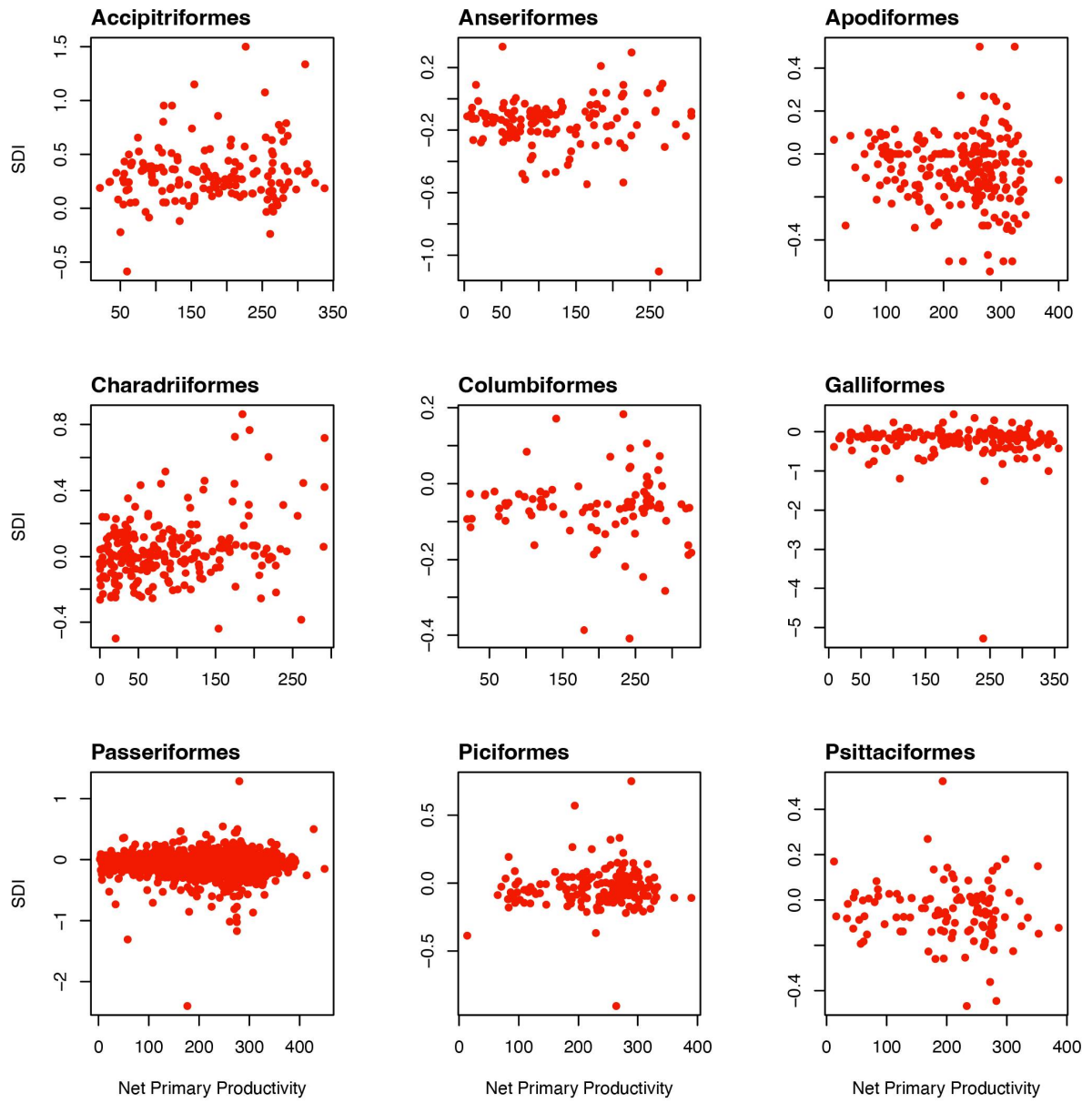**Figure S6**. Relationship between precipitation seasonality and the degree of SSD.

Figure S7. Relationship between net primary productivity and the degree of SSD.

EPÍLOGO

Nesta dissertação, abordamos a evolução do tamanho do corpo e do dimorfismo sexual em vertebrados terrestres. No Capítulo I, buscamos identificar padrões gerais na evolução do tamanho do corpo entre anfíbios, squamata, aves e mamíferos, investigando se essa evolução segue um modelo de taxas de evolução constante ao longo do tempo e se existem generalidade entre os grupos estudados. No Capítulo II, concentramos nossa análise na evolução do dimorfismo sexual de tamanho em aves, aproveitando a ampla disponibilidade de dados nesse grupo. Nessa parte, investigamos a relação entre a evolução do tamanho do corpo e do dimorfismo sexual, bem como os correlatos espaciais e ecológicos que influenciam a ocorrência do dimorfismo. Com esse estudo, esperamos contribuir para o entendimento dos padrões macroevolutivos do tamanho corporal em vertebrados terrestres.

Ao explorar as diferenças na evolução do tamanho corporal em vertebrados terrestres, encontramos suporte para desvios consistentes de um modelo de taxa constante em todos os clados, sugerindo que a evolução do tamanho corporal pode ser caracterizada por padrões semelhantes em vertebrados terrestres. Dentre esses padrões, podemos citar a heterogeneidade das taxas de evolução entre linhagens de um mesmo clado, a relação positiva entre taxa de evolução e tamanho de corpo e o aumento dessas taxas em tempos evolutivos mais recentes. Além disso, embora os ectotermos tendam a ter tamanhos corporais menores que os endotermos, suas taxas de evolução não mostraram diferenças substanciais, contrariando hipóteses da literatura que relacionam tamanho de corpo dos animais e suas formas de adquirir calor. Em conjunto, esses resultados sugerem que podem existir princípios gerais que regem a evolução do tamanho corporal em vertebrados terrestres, embora os mecanismos subjacentes ainda sejam pouco compreendidos.

Nossos resultados demonstraram também que a evolução do dimorfismo sexual de tamanho em aves provavelmente é influenciada por diversos fatores, sendo a seleção sexual, a seleção por fecundidade em fêmeas e a divergência de nicho entre sexos de especial importância em diferentes ordens de aves. No entanto, não encontramos evidências de que fatores ambientais, como sazonalidade de temperatura, produtividade e latitude, sejam bons preditores do dimorfismo sexual. O que este estudo indica é que o surgimento do dimorfismo sexual de tamanho em aves é multifatorial, porém com pouca influência climática a este nível taxonômico.

Esperamos que estudos futuros se concentrem em descrever como outros aspectos da evolução do tamanho corporal também podem ser comuns a vertebrados terrestres e se os padrões encontrados em nosso estudo para o dimorfismo sexual de tamanho podem se aplicar a outros grupos de organismos. Além disso, estudos futuros, com foco em escalas espaciais e temporais alternativas, podem proporcionar maior compreensão das diferenças dos mecanismos preditores do dimorfismo sexual de tamanho observadas entre os táxons. Por fim, reforçamos a importância de uma abordagem macroevolutiva explícita para entender os fatores que influenciam o tamanho de corpo e o dimorfismo sexual de tamanho.

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