

1 **Sexes and species as rival units of niche saturation during community assembly**

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16 **Key words:** Adaptive radiation, speciation, divergent selection, sexual dimorphism, ecological opportunity,
17 niche-packing, lizards, *Liolaemus*

18 **Short Running Title:** Sexes and species compete to fill niches

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30 **Abstract**

31 **Aim:** Community assembly is traditionally assumed to result from speciation and colonisation mediated by
32 available niche space. This paradigm is expanded by the theory that niche space can also be saturated by
33 intersexual adaptive divergence (ecological sexual dimorphism) when interspecific competition is relaxed. This
34 theory (here termed 'niche-packing equivalence') predicts that the evolution of ecological sexual dimorphism
35 constrains the ecological opportunity that would otherwise lead to ecological speciation or colonisation, and that
36 saturation of niches by different species constrains divergent selection for divergence between the sexes.
37 Therefore, sexes and species are equivalent, yet antagonistic units of niche occupation. We present the most
38 comprehensive test of the niche-packing equivalence theory at ecological timescales (assemblage level) to date.

39 **Location:** South America

40 **Major taxa:** *Liolaemus* lizards.

41 **Methods:** We identified 23 *Liolaemus* assemblages varying in species-richness and sexual size dimorphism
42 (SSD), distributed across a wide environmental range. We used mixed effects models, permutation tests and
43 MCMC regressions to quantify the relationship between SSD and species-richness. We then partitioned the
44 body size niche dimension between the sexes and among species, and tested for non-overlapping body size
45 distributions. We regressed SSD and species-richness of each assemblage against environmental predictors,
46 using multi-model inference and structural equation modelling.

47 **Results:** Sexual dimorphism declines with increasing species-richness, and a strong signal of tension between
48 the two remains following phylogenetic control. This pattern is accompanied by evidence of constraints on body-
49 size partitioning among species and between the sexes: the two units of niche saturation tend not to overlap.
50 However, across assemblages, species-richness and SSD correlate with different environmental variables,
51 suggesting that their tension is context-specific.

52 **Main conclusions:** Our evidence supports the prediction that sexual dimorphism and species-richness are
53 alternative outcomes of adaptive radiation. However this antagonism is mediated by a suite of environmental
54 predictors that influence dimorphism and species-richness differentially.

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59 Introduction

60 The adaptive proliferation of biodiversity results from divergent natural selection driving niche expansions in
61 species exposed to ecological opportunity – a process potentially leading to speciation (Schluter, 2000;
62 Gavrillets, 2004; Nosil, 2012). Therefore, a prevailing paradigm in evolutionary ecology is that the distribution of
63 biodiversity is shaped by the diversity-dependent accumulation of species that compete to saturate niche space
64 (Losos, 2010). However, saturation of ecological opportunity by newly evolving species can be replaced by
65 adaptive divergence between the sexes of the same species (ecological sexual dimorphism). According to this
66 idea, intersexual niche expansions are promoted by disruptive natural selection when sexual conflict arising from
67 resource competition is mitigated by the evolution of dimorphic males and females adapted to non-overlapping
68 regions of the niche landscape (e.g., Fairbairn *et al.*, 2007), in environments where the intensity of interspecific
69 competition declines with decreasing numbers of competitors (Slatkin, 1984; Bolnick & Doebeli, 2003).

70 Accumulating evidence suggests that the evolution of ecological sexual dimorphism can influence, or be
71 influenced by the trajectories and rates of biodiversity proliferation on macroevolutionary timescales (i.e., when
72 rates of speciation within a lineage are associated with the degree of sexual dimorphism at phylogenetic nodes)
73 and on microevolutionary and ecological timescales (i.e., when species richness, whether resulting from
74 speciation or colonisation, is associated with the degree of sexual dimorphism in resident species). The
75 proliferation of sexually dimorphic species is predicted to saturate morphospace, thus increasingly limiting the
76 opportunities for lineages to radiate adaptively via niche filling (Schoener, 1977; Losos, 2009; De Lisle & Rowe,
77 2015). In any given assemblage, the saturation of niche space by an increasing number of species is expected
78 to limit opportunities for the evolution of ecological sexual dimorphism, while niche saturation by dimorphic
79 species might constrain colonisation by additional species (Bolnick & Doebeli, 2003; Butler *et al.*, 2007).
80 Therefore, this 'niche-packing equivalence' theory predicts that ecologically distinct species and dimorphic sexes
81 operate as rival units of niche saturation during adaptive radiations or community assembly, which leads to
82 ecological and evolutionary tension between the two forms of diversification as each of them contributes to
83 saturation of the ecological opportunity (Slatkin, 1984; Bolnick & Doebeli, 2003).

84 The underappreciated, yet fundamental role for ecological sexual dimorphism in influencing the
85 trajectories of lineage diversification and assemblage evolution has received limited attention that has resulted in
86 mixed support. At macroevolutionary timescales, the only known study (De Lisle & Rowe, 2015) presented
87 robust evidence rejecting the core prediction that lineage diversification rates decay with increasing sexual

88 dimorphism. Based on a global-scale amphibian analysis, these authors showed that increasing sexual size
89 dimorphism (SSD) is associated with increases in speciation rates, and decreases in extinction rates. At
90 assemblage level, a few studies have revealed conflicting evidence. On the one hand, a small number of studies
91 on *Anolis* lizards (Schoener, 1969, 1977; Butler *et al.*, 2007; Poe *et al.*, 2007) and turtles (Stephens & Wiens,
92 2009), have shown negative correlations between species-richness and sexual dimorphism, consistent with
93 niche-packing equivalence theory. In contrast, a global-scale study investigating the effect of insularity and
94 species-richness on the degree of sexual dimorphism across island mammals and lizards (Meiri *et al.*, 2014)
95 failed to identify a relationship between the two forms of diversity. Such disparate results across studies may be
96 caused by their extreme differences in spatial and taxonomic scale. At very large scales (e.g., Meiri *et al.*, 2014),
97 selection may result from competition across multiple resource axes, thus potentially dissipating the predicted
98 impetus of univariate selection operating on a specific trait that may be pushed to diverge to mitigate intersexual
99 conflict via evolution of sexual dimorphism (Cooper *et al.*, 2011). In addition, De Lisle & Rowe (2015) suggested
100 that the signal of competition is more likely to be identified at finer scales (such as in the *Anolis* studies), while
101 taking into account proxies of the ecological opportunity under which diversification dynamics occur. Such
102 proxies might include the availability of different levels of resources to accommodate ecologically different sexes
103 or species, or the occupation of distinct portions of morphospace. No such quantitative tests of the niche-packing
104 equivalence theory exist.

105 In this study, we present the most comprehensive test of the ecological-scale version of the niche-
106 packing equivalence theory that community assembly is mediated by an antagonistic tension between the
107 degree of sexual dimorphism and species-richness, as a function of available niche space. Using multiple
108 assemblages of *Liolaemus* lizards (Pincheira-Donoso *et al.*, 2015), one of the world's most prolific vertebrate
109 radiations (Pincheira-Donoso *et al.*, 2013b; Pincheira-Donoso *et al.*, 2013a), we implemented a test that
110 investigates the theory at a fine taxonomic scale, but at large spatial and environmental scales, and includes
111 measures of microhabitat availability across assemblages. Following control of phylogenetic effects, we reveal
112 the predicted negative covariation between sexual dimorphism in body size and species-richness across
113 assemblages. We then use body size distributions per species to test whether sexes and species occupy distinct
114 portions of the body-size phenotypic dimension. We also test whether species-richness and SSD share similar
115 sets of environmental predictors.

116

117 **Materials and methods**

118 ***Assemblage selection***

119 We studied 23 *Liolaemus* assemblages consisting of one to five species (Supplementary Figure S1;
120 Supplementary Table S1). Our assemblages occur on the western side of the Andes mountain range in Chile,
121 where ~85% of lizard species (90+ species) belong to this clade (Pincheira-Donoso *et al.*, 2008b; Pincheira-
122 Donoso *et al.*, 2017), and in Argentinean Patagonia, where multiple independent lizard invasions of high-
123 elevation plateaus ('Mesetas') have resulted in isolated assemblages (Cei, 1986; Scolaro, 2005; Pincheira-
124 Donoso, 2011). Boundaries of assemblages were determined by geographic (e.g., mountains, valleys, rivers)
125 and/or ecological features (e.g., desert assemblages isolated in vegetation patches). In addition, published
126 distributional data (e.g., Cei, 1986; Pincheira-Donoso & Núñez, 2005) and over 8,000 museum records provided
127 the original basis for identification of independent assemblages. Data obtained from field explorations carried out
128 over ten years (by DP-D) provided 4,000 further geographic data points that confirmed our conclusions about
129 assemblage isolation. Five species in our dataset were represented in a maximum of two different assemblages
130 (see Table S1, for species names). A few other *Liolaemus* assemblages host 6-8 coexisting species, but given
131 the lack of clear boundaries among these and other assemblages (e.g., substantial spatial overlap among
132 species with large geographic ranges) they were excluded from the analyses to avoid a decay in the spatial
133 control over species interactions and thus, of our proxy for the intensity of competition (e.g., see Butler *et al.*,
134 2007; Losos, 2009). Finally, all our studied lizard assemblages are dominated by (or consist exclusively of)
135 *Liolaemus* species, avoiding the competitive effects that lizards of other lineages, with potentially similar
136 ecological requirements, might exert within each assemblage.

137

138 ***Sexual size dimorphism data***

139 Body size data were collected for all species found in the 23 studied assemblages. Snout-vent length (SVL) is
140 the standard estimator of body size in lizards (Meiri, 2008; Pincheira-Donoso *et al.*, 2011). Hence, we used this
141 proxy to quantify the extent of sexual size dimorphism. Given that body size in lizards follows asymptotic growth
142 curves, the use of the largest available/known specimen or the use of the average calculated from the entire
143 sample can overestimate or underestimate, respectively, adult body sizes (Stamps & Andrews, 1992; Brown *et al.*,
144 1999). Therefore, from the entire available sample of adult specimens (Pincheira-Donoso & Núñez, 2005;
145 Pincheira-Donoso & Tregenza, 2011), we obtained the mean of the largest two-thirds of each sample per sex,

146 per species, and per assemblage, which provides an intermediate SVL value (between the mean and maximum
147 known for each sex), and hence, a more reliable estimate of adult body size (Losos *et al.*, 2003; Pincheira-
148 Donoso *et al.*, 2008a). Subsequently, the degree of SSD was calculated with the formula $\ln(\text{SVL}_{\text{Male}}/\text{SVL}_{\text{Female}})$.
149 This measure of dimorphism is intuitive and has been shown to perform with satisfactory statistical power (Smith,
150 1999; Fairbairn, 2007). The fundamental prediction of the theory is that the extent of sexual dimorphism varies
151 as a function of assemblage species-richness. SSD estimates for the five *Liolaemus* species found in two
152 assemblages (see Supplementary Table S1) were therefore calculated based on the actual specimens recorded
153 at each specific assemblage, separately.

154

155 ***Relationships between SSD and species-richness***

156 We tested for a tension between interspecific and intraspecific adaptive diversity by correlating or regressing
157 SSD against species-richness, across our 23 assemblages. Different approaches can be taken to this analysis,
158 each with strengths and weaknesses. The simple correlation between assemblage species-richness and SSD
159 (the mean SSD across all species in the assemblage) is conservative, but excludes information on the individual
160 SSD values for each species. The correlation between species-richness and individual species' SSD ignores the
161 non-independence of species nested within assemblages. Accounting for "assemblage identity" as a random
162 effect to avoid this pseudoreplication obliged us to use regression models that assumed no uncertainty in the
163 predictor, species-richness. We present per-assemblage, per-species, and mixed-effects versions of these
164 analyses, and control for artefactual relationships by permuting (shuffling) species randomly among
165 assemblages. For each analysis, the slope or correlation coefficient of the observed relationship was compared
166 to the null distribution of slopes based on 10K permutations, concluding statistical significance if the observed
167 correlation parameter lies in the upper or lower 2.5th centiles of the null distribution. These analyses were
168 adjusted for data quality and precision by weighting them by the sample sizes used to calculate sexual
169 dimorphism for each species.

170

171 ***Controlling for phylogenetic non-independence***

172 Recognising that observed correlations between SSD and species-richness could be due to phylogenetic
173 patterns of SSD coupled with phylogenetically biased co-occurrences of species in assemblages, we repeated
174 our per-species regression analyses using phylogenetic control on the residuals. There exists a well-developed

175 phylogeny for many *Liolaemus* species (Pincheira-Donoso *et al.*, 2013a; Pincheira-Donoso *et al.*, 2015), but only
176 half of the species in this study are represented as tips. We created a proxy phylogeny by associating
177 unrepresented species with sister species or closest relatives that appear in the established phylogeny. This
178 proxy phylogeny (Supplementary Figure S2; Supplementary Table S3) contains tips that can each represent
179 multiple “real” species in our dataset. This required us to account for the influence of phylogeny using a Monte
180 Carlo Markov Chain (MCMC) generalised linear mixed effect regression model, which considered species
181 identity, assemblage identity and proxy phylogeny as random effects. We used the MCMCglmm package in R,
182 and employed parameter expansion of our three random effects to ensure convergence. MCMC chains were run
183 for 100K iterations with a burn-in of 10K and a thinning interval of 100. We report the posterior distributions of
184 variance absorbed by phylogeny, and slope of the relationship between sexual dimorphism and species-
185 richness.

186

187 ***Relationships between body size distributions and species-richness***

188 We explicitly tested our assumption that species in species-poor assemblages occupy larger niches than species
189 in species-rich assemblages by examining the predicted negative correlation between species-richness and the
190 breadth of their body size distributions (measured as the standard deviation of SVL). As with analyses of SSD
191 above, we tested this correlation per-assemblage, using the mean of the body size standard deviations across
192 species. We then modelled the slope of the relationship between per-species body size standard deviation and
193 species-richness, absorbing assemblage as a random effect. All analyses were partnered with permutation tests
194 that shuffled species among assemblages 10K times to create a histogram of test statistics under the null
195 hypothesis of no correlation/relationship. Recognising that dimorphic species are predisposed to having broader
196 body-size distributions, we repeated these tests separately for males and for females. This provides a check that
197 changes in body-size distributions are due to sexual dimorphism, not expansion of each sex’s size distribution.

198

199 ***Partitioning body size variation between sexes and species***

200 The hypothesis that correlations between SSD and species-richness are driven by constraints on body size
201 distributions (driven by size-dependent competition) predicts that, within assemblages, there should be a
202 negative relationship between the proportion of variance in body size explained by partitioning among species
203 and that explained by partitioning between the sexes. We expect a negative relationship between these

204 variance components by default (because where more variance is explained by one component, less is available
 205 to be explained by the other). However, residual variance, which describes the overlap in body size distributions
 206 between sexes and among species, also contributes to total variation. If the tension between SSD and species-
 207 richness forces those ecological units into distinct portions of the body size niche dimension, then natural
 208 assemblages should lie closer to the line of perfect negative covariance than artificial assemblages made by
 209 shuffling combinations of species.

210 To test this prediction we performed a factorial analysis of variance in body size against sex (male or
 211 female) and species identity (one to five species), for each assemblage. We recorded the proportions of variance
 212 (R^2) explained by sexes and species, and the proportion left unexplained, then modelled the nonlinear
 213 relationship between R^2_{sexes} and R^2_{species} . Because $R^2_{\text{sexes}} + R^2_{\text{species}}$ cannot be greater than 1, this relationship is
 214 constrained to lie below the hypotenuse between [0,1] and [1,0]. Assemblages lying along the line are those in
 215 which all of the variation in body size is explained by a combination of sex- and species-identity effects.
 216 Assemblages lying closer to [0,0] are those in which body size distributions overlap considerably between sexes
 217 and among species (Figure 3). The null hypothesis for this analysis is that the natural assemblages of *Liolaemus*
 218 lie no closer to the $R^2_{\text{sexes}} + R^2_{\text{species}} = 1$ hypotenuse than random assemblages of lizard species. We tested
 219 departure from this expectation by shuffling species among assemblages 10K times and repeating the factorial
 220 ANOVA analyses for each shuffle. This approach combines the influence on niche saturation of divergence
 221 among species, and divergence between sexes. To test the influence of species divergence alone, we shuffled
 222 the size-differences among species, but constrained the size-differences between sexes to be as observed in
 223 the data. To test the influence of sexual divergence alone, we shuffled the size-differences between sexes,
 224 among species, but constrained the size-differences among species to be as observed in the data. Simulations
 225 of simplified assemblages occupying body size niches according to four simple rule-sets (a) random assembly of
 226 species and sexes; b) species occupy available niches preferentially, but sexual divergence is random; c)
 227 species occupy niches randomly, but sexual divergence occurs when niches are available; d) species and sexes
 228 both diverge into available niches) confirmed that these constrained shuffles correctly revealed niche-packing
 229 patterns due to sexual or species divergence (see supplementary material).

230 For the observed data and each shuffle (total shuffle; species shuffle; sex shuffle), we modelled the
 231 distance of R^2_{sexes} vs. R^2_{species} from the hypotenuse, in two ways. First, we calculated the mean deviation of
 232 perpendicular residuals from the hypotenuse. Second, recognising that shuffled assemblages with overlapping

233 body size distributions lay closer to [0,0] than observed assemblages, and that data close to [0,0] naturally lay
 234 furthest from the hypotenuse, we used least-squares nonlinear regression to test the curvature of the quadratic
 235 fit to observed or simulated variance components that joined the constrained intercepts of [0,1] and [1,0]. The
 236 quadratic function that links x (the distance along the hypotenuse) to y (the perpendicular distance of [R^2_{species} ,
 237 R^2_{sexes}] from x), is $y = b(\sqrt{2}x^2 - 2x)$, where b describes the intensity of curvature (see Figure 3). Both sets of
 238 analyses weighted the contribution of real and shuffled assemblages by the residual degrees of freedom of the
 239 associated ANOVA used to calculate R^2_{sexes} and R^2_{species} . We compared the observed outcome (mean deviation
 240 from the hypotenuse; curvature of the quadratic) to the empirical null distributions of these parameters based on
 241 our shuffles, and calculated p-values based on the quantile position of the observed parameters (Figure 3).

242

243 ***Sexual dimorphism: sexually or naturally selected?***

244 Although not essential to the expanded niche-packing equivalence theory, we note that if SSD is driven by
 245 ecological opportunity alone, there should be no trend for dimorphism to be consistently male- or female-biased.
 246 Alternatively, if SSD is driven by sexual selection, we might expect males to be consistently larger than females,
 247 or vice versa. We tested this with a simple paired t -test of mean body size between males and females, across
 248 species. We checked the robustness of this result to phylogenetic control, by fitting an intercept-only
 249 MCMCglmm, with SSD as response variable, using the proxy phylogeny, and all MCMC settings as described
 250 above.

251

252 ***Environmental estimators of niche space abundance***

253 Different environments are expected to provide different diversities of potential niches to be constructed or
 254 exploited (Peterson *et al.*, 2011). Since the assemblages we sampled are widely spread along a ~3800 km
 255 latitudinal range, the availability of niche space is likely to vary across these assemblages, creating variation in
 256 their potential to host different numbers of ecological units, whether different species or divergent sexes within
 257 species. To examine this variation, we regressed SSD and species-richness against a number of environmental
 258 factors as proxies for niche diversity per assemblage. First, exclusively based on field observations, we
 259 quantified the numbers of microhabitats and the amount of vegetation available per assemblage site. Six
 260 microhabitat categories were identified in the areas occupied by *Liolaemus* (boulders, rocky ground, open
 261 ground, bushy ground, grassland, and trees) (Schulte *et al.*, 2004; Pincheira-Donoso *et al.*, 2009), which were

262 each scored as rare (0), relatively common (0.5) or common (1). We summed these scores across microhabitat
263 categories to yield a “microhabitats” index ranging from zero to six. Vegetation indices ranged from zero (little or
264 no vegetation) to three (high cover of thick scrub) with intervals of 0.5. We then employed two proxies of
265 resource abundance (Costa *et al.*, 2007; Pincheira-Donoso & Meiri, 2013; Novosolov *et al.*, 2016): mean annual
266 precipitation (on a spatial resolution of 1/6°), assumed to be positively associated with productivity in the areas
267 we study; and NPP, an estimate of the net amount of solar energy converted to plant organic matter through
268 photosynthesis, measured in units of elemental carbon per year, on a spatial resolution of 1/4°. Precipitation
269 data came from Worldclim (Hijmans *et al.*, 2005) and NPP data (log-transformed) came from Imhoff *et al.* (2004).
270 These climatic data were assigned to each studied community by intersecting the geographical centroids of the
271 assemblages with the above climatic layers in ArcGIS 9.3.1. To quantify the influence of environmental factors
272 on SSD and species-richness, we performed multiple regression analysis of mean responses per assemblage
273 against NPP, annual precipitation, latitude, altitude, vegetation and microhabitat diversity, all scaled to have zero
274 mean and unit variance. We used Akaike Information Criteria and Akaike model weights, and dredged the full
275 model to determine the best model and the difference in AIC for each possible subset model using the R
276 package ‘MuMIn’ (Barton, 2017). This full set of models was averaged, with parameters weighted by Akaike
277 model weights, to provide means and 95% confidence intervals for the model-averaged effect sizes of each
278 predictor. Phylogenetic control is not applicable to these analyses because we use assemblage-level, rather
279 than species-level metrics. We then used Structural Equation Modelling (SEM), using the R package ‘sem’ (Fox
280 *et al.*, 2017), to tease apart the relationship between environment, SSD and species richness. We used the
281 subset of environmental predictors, identified by our multiple regressions as having significant influence on the
282 response variables. We treated these as predictors, and considered three SEMs: first, a model in which
283 environmental variables predicted SSD and species richness independently, but with residual covariance
284 between these two responses; second, environmental variables predicted SSD which in turn predicted species
285 richness; third, environmental variables predicted species richness which in turn predicted SSD. We used a
286 combination of significance tests and AIC to compare these models, statistically.

287

288 **Results**

289 ***Relationship between sexual size dimorphism and species-richness***

290 As predicted, the magnitude of SSD correlated negatively with the number of *Liolaemus* species per assemblage
 291 (Figure 1). As numbers of coexisting species per assemblage increased, there was a significant decrease in the
 292 average degree of SSD per assemblage (Pearson's correlation; $\rho = -0.430$, $t_{21} = -3.226$, $P = 0.004$; permutation
 293 test P -value 0.003; Figure 1a). Correlation analysis using each species confirmed this result ($\rho = -0.387$, $t_{53} = -$
 294 3.057 , $P = 0.003$; permutation $P = 0.002$), as did mixed effects regression of SSD against species-richness,
 295 weighted by sample size for each species (slope = -0.43 , $F_{1,21} = 12.03$, $P = 0.002$; permutation $P = 0.001$; Figure
 296 1b). These patterns were robust (P remained < 0.05) to the removal of an influential single-species assemblage
 297 with high SSD (the Arica assemblage, Figure 1a, b). Indeed, P -values were < 0.1 for analyses that completely
 298 removed all single-species assemblages (although it would be difficult to justify such extreme data pruning).
 299 Phylogenetic mixed-effects regression revealed credible phylogenetic signal in the residuals of this model
 300 (Figure 1c), but the posterior distribution of the slope of sexual dimorphism against species-richness was
 301 negative with 96.3% probability (Figure 1d). The variances due to assemblage and species identities were not
 302 credibly greater than zero.

303

304 ***Correlation between breadth of body size distribution and species-richness***

305 The negative correlation between SSD and species-richness was accompanied by a significant negative
 306 correlation between the average breadths of body size distributions per species, and species-richness per
 307 assemblage (Pearson's correlation; $\rho = -0.432$, $t_{21} = -2.198$, $P = 0.039$; permutation test P -value 0.019; Figure
 308 2a). This relationship held when the correlation was tested using each species in each assemblage, and when
 309 modelled as a regression with a random effect of assemblage identity ($\rho = -0.323$, $t_{53} = -2.483$, $P = 0.016$;
 310 permutation $P = 0.004$; slope = -0.430 , $F_{1,21} = 6.167$, $P = 0.022$; permutation $P = 0.006$) (Figure 2b). However, no
 311 significant relationship existed between the breadths of body size distributions per sex and species-richness (per
 312 assemblage correlations: male body size $\rho = 0.215$, $t_{21} = 1.012$, $P = 0.323$, Figure 2c; female body size $\rho =$
 313 0.191 , $t_{21} = 0.891$, $P = 0.383$, Figure 2d). All of these results were supported by MCMCglmm models that
 314 controlled for phylogenetic signal. Indeed, we found no credible evidence for phylogenetic signal in the breadth
 315 of body size distributions per species, nor per sex per species.

316

317 ***Constrained partitioning of body size variation between sexes and species***

318 The proportion of variance in body size explained by intersexual divergence decreased as the proportion
319 explained by interspecific divergence increased (Figure 3a). More importantly, we found support for the
320 prediction that this relationship is more intense (i.e., the observations lay closer to the line of perfect constraint;
321 Figure 3b) than for the vast majority of shuffled lizard assemblages created to define the expectation under the
322 null hypothesis (see results in Supplementary Analysis S2, and Table S2). The mean deviation of the observed
323 partition of body size variation from the line of perfect constraint was too small to fit the null hypothesis
324 distribution (permutation $P < 0.001$; Figure 3c). Constrained shuffles revealed that niche-packing as measured
325 by this deviation was due to a combination of species divergence ($P = 0.014$) and sexual divergence ($P = 0.001$).
326 Least squares nonlinear regression of observed and shuffled assemblages confirmed that the observed
327 curvature in the quadratic line joining the intercepts of “all intersexual variation” and “all interspecific variation”
328 (Figure 3b) was too small to fit the null hypothesis (permutation $P = 0.001$; Figure 3d). Constrained shuffles
329 revealed that niche-packing, as measured by curvature, was due to a combination of species divergence ($P =$
330 0.049) and sexual divergence ($P = 0.01$). This provides clear evidence that natural *Liolaemus* assemblages are
331 structured such that the negative association between intersexual and interspecific body size variation is closer
332 to the perfect constraint than expected by chance. Sexes and species both tend to occupy distinct portions of the
333 body size niche dimension when niche opportunities exist, and appear to constrain each other’s divergence or
334 colonisation.

335

336 ***Is SSD generally naturally or sexually selected?***

337 We found that male *Liolaemus* lizards were consistently larger than females (Pincheira-Donoso & Tregenza,
338 2011), across species (paired t -test, $t_{54} = 6.692$, $p < 0.001$; Figure S3). SSD showed credible evidence of
339 phylogenetic signal, but having controlled for this, mean SSD was credibly male-biased among species (99.3%
340 of posterior samples of mean SSD were > 0). This indicates that the initial source of SSD is linked to sexual
341 identity, either via direct sexual selection or via a predisposition for males to evolve large (or females to evolve
342 small) body size.

343

344 ***Environmental predictors of species-richness and SSD***

345 Our analyses of candidate environmental drivers using model-averaged regressions of SSD against
346 environmental predictors revealed SSD declined with increasing amounts of vegetation, and with increasing

347 latitude (Figure 4a). Similar analyses of species-richness against environmental predictors revealed the only
348 statistically important predictor to be annual precipitation: species-richness increased with increasing rainfall
349 (Figure 4b). Structural equation modelling confirmed the minimal adequate set of environmental predictors (SSD
350 influenced by latitude and vegetation; species richness influenced by rainfall; Table 1), and furthermore revealed
351 that the negative correlation between SSD and species richness remains significant following control of
352 environmental influences. Rival models, in which SSD predicted variation in species richness, or vice versa,
353 were not supported in our SEMs (Table 1). Overall, the bivariate correlation between SSD and species richness
354 remains significant, but each response is mediated by different environmental predictors.

355

356 **Discussion**

357 Our study provides a large-scale test of the niche-packing equivalence theory, at assemblage level and
358 ecological timescales, that dimorphic sexes and species are rival units of niche-saturation during adaptive
359 radiations and community assembly (Slatkin, 1984; Bolnick & Doebeli, 2003; Butler *et al.*, 2007). As predicted,
360 our analyses reveal a negative relationship between the species-richness of lizard assemblages and the
361 magnitude of SSD in their component species. Additionally, although we observed that the breadth of the body
362 size distribution per species is constrained by species-richness, the evidence for the opposite pattern of species-
363 richness constraining the size distribution breadth of either sex alone is non-significant, raising the possibility that
364 there is an asymmetry in the effect of these variables on one another. Finally, our variance decomposition
365 analyses confirm that *Liolaemus* assemblages are organized non-randomly such that body size variation is
366 constrained to be partitioned into the “between-sexes” and “among-species” components: increases in one
367 component are accompanied by decreases in the other.

368 The patterns of phenotypic organization among and within species that we observe are also related to
369 bioclimatic variation across assemblages. Species-richness increases with increasing precipitation across
370 assemblages, presumably indirectly through its influence on vegetation and associated trophic levels that form
371 the diet of *Liolaemus* species (greater dietary diversity facilitates higher numbers of coexisting species given the
372 greater niche space). In contrast, while SSD is not influenced by rainfall, it increases with decreasing vegetation
373 complexity and with increasing southerly latitude. Therefore, SSD seems to be favoured in low-complexity, low
374 productivity environments. The latitudinal cline, however, remains unexplained. Our combined findings reveal a
375 scenario consistent with a relationship between SSD and species-richness mediated by the environmental

376 conditions that influence variation in available niche space per assemblage. However, despite these effects from
377 agents of natural selection, it remains possible that sexual dimorphism has been influenced by sexual selection
378 (see Andersson, 1994). Niche packing occurs against the backdrop of sexual selection on size dimorphism, with
379 the potential for interactions between the two (for instance, where factors such as population density and
380 species richness impact both ecological competition for resources and inter-male competition for mates). The
381 action of sexual selection during the evolutionary histories of *Liolaemus* species presumably predisposes them
382 to evolve dimorphism in the direction of males being larger than females, but our results suggest that this size
383 difference is constrained in species-rich assemblages. We note that sexual dimorphism is greatest in habitats
384 with low cover or complexity of vegetation, and suggest that this could be due to the importance of sexual
385 signaling in simple habitats where visibility makes selection on display traits more intense, or due to more
386 intense competition for scarce food resources.

387 Our core questions were (1) whether ecologically distinct sexes and species can saturate niches in
388 equivalent ways, and hence, (2) whether such equivalence triggers the predicted conflict between sexual
389 dimorphism and species-richness (Bolnick & Doebeli, 2003; Butler *et al.*, 2007). Our results reveal patterns
390 consistent with the prediction that sexual dimorphism and species-richness are antagonistic. However,
391 environments where resource availability is higher sustain more species, while highly dimorphic species are
392 found in environments of low vegetation cover or complexity. Overall, despite strong evidence for a negative
393 correlation between SSD and species-richness, we conclude that this tension is context-specific in *Liolaemus*.

394 Our surveys of sexual dimorphism and species richness did not allow us to determine cause and effect,
395 i.e., whether the two sources of body size variation compete equally for niche space during the processes of
396 adaptive radiation and community assembly. We suggest that variation among species is more likely to constrain
397 the evolution of sexual dimorphism, than *vice versa*, for two main reasons. First, sexual dimorphism is
398 evolutionarily more labile than species formation (i.e., it evolves faster, requires simpler conditions, is reversible),
399 perhaps because it requires only a direct effect of selection on ecological traits, rather than an additional indirect
400 effect on mating behaviour (Bolnick & Doebeli, 2003; Cooper *et al.*, 2011). Second, the magnitude of ecological
401 divergence between the sexes is typically small compared to the magnitude of ecological divergence among
402 coexisting species. Hence, we argue that whenever niche space has not been saturated by other species,
403 sexual dimorphism of ecologically relevant phenotypes may evolve by natural selection through its benefits for
404 sex-specific fitness. Such benefits may include, for example, reduced intensity of resource competition between

405 the sexes (Shine, 1989; Bolnick & Doebeli, 2003), and relaxation of intralocus sexual conflict when intrinsic sex-
406 specific fitness-linked roles need to evolve in different directions under the same natural selection regimes
407 (Hedrick & Temeles, 1989; Bonduriansky & Chenoweth, 2009). Any attempt to tease apart the influence of
408 species richness on the evolution of sexual dimorphism and/or the colonisation of dimorphic species, from the
409 influence of sexual dimorphism on speciation and/or the colonisation of new species, would require either
410 massive-scale experimentation, or long-term observation of evolutionary and ecological event sequences.

411 Our results suggest interesting nuances to the relationship between sexual dimorphism and adaptive
412 radiation. De Lisle & Rowe (2015) show that sexual dimorphism is associated with diversification rate and
413 reduces extinction, hence promoting biodiversity on macroevolutionary timescales. Consequently, such positive
414 impacts on radiation would be compromised when the pressures of interspecific competition prevent divergence
415 between the sexes. The niche-packing equivalence theory raises novel possibilities to understand eco-
416 evolutionary dynamics by incorporating the role of intraspecific diversification into the traditionally species-
417 centred views of biodiversity evolution and community assembly.

418

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426

427 **Biosketch**

428 Daniel Pincheira-Donoso is a Senior Lecturer in Evolutionary Biology. His research investigates the role of
429 selection as a driver of adaptive diversity, with a primary focus on the interplay between the emergence of
430 adaptive traits and their impact on large-scale patterns of diversity.

431

432 **Data Accessibility**

433 The data supporting the results will be archived in an appropriate public repository such as Dryad or Figshare
 434 and the data DOI will be included at the end of the article.

435

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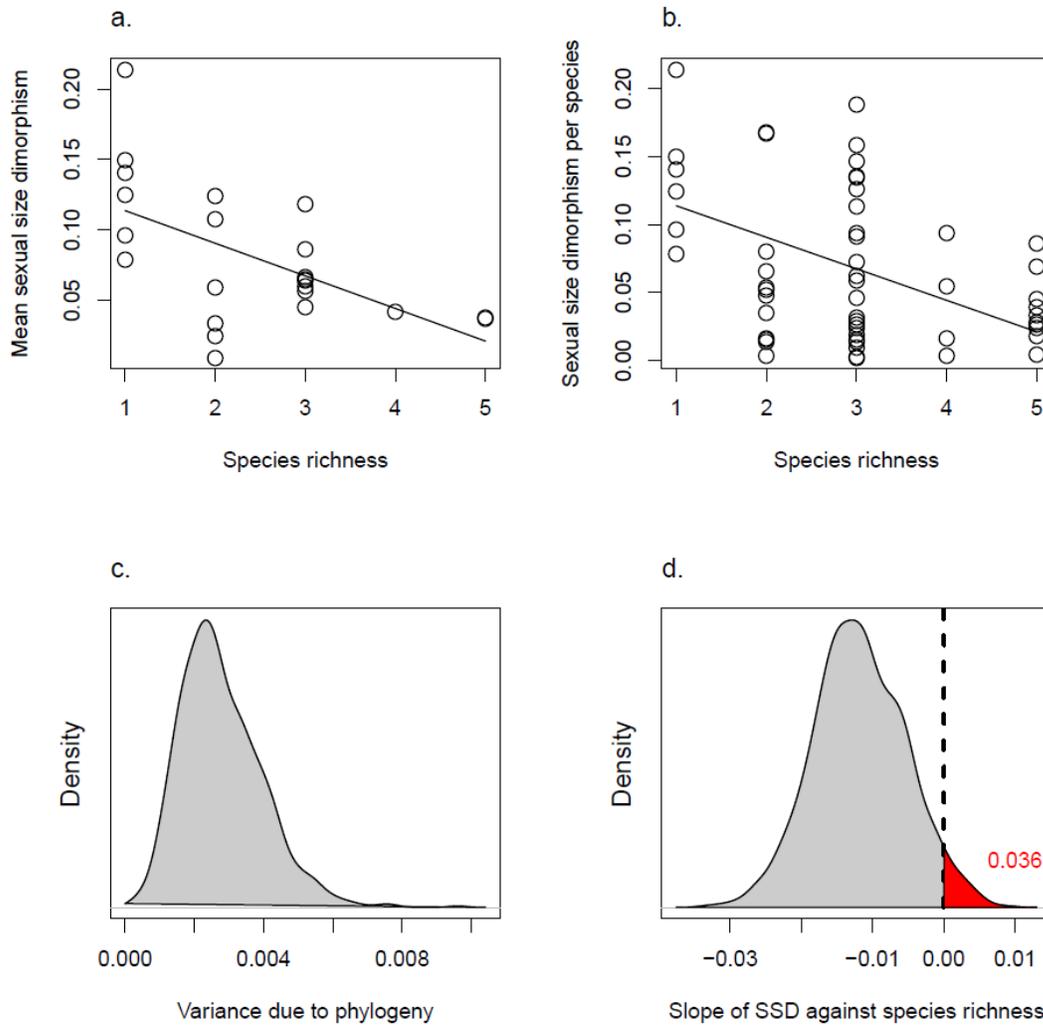
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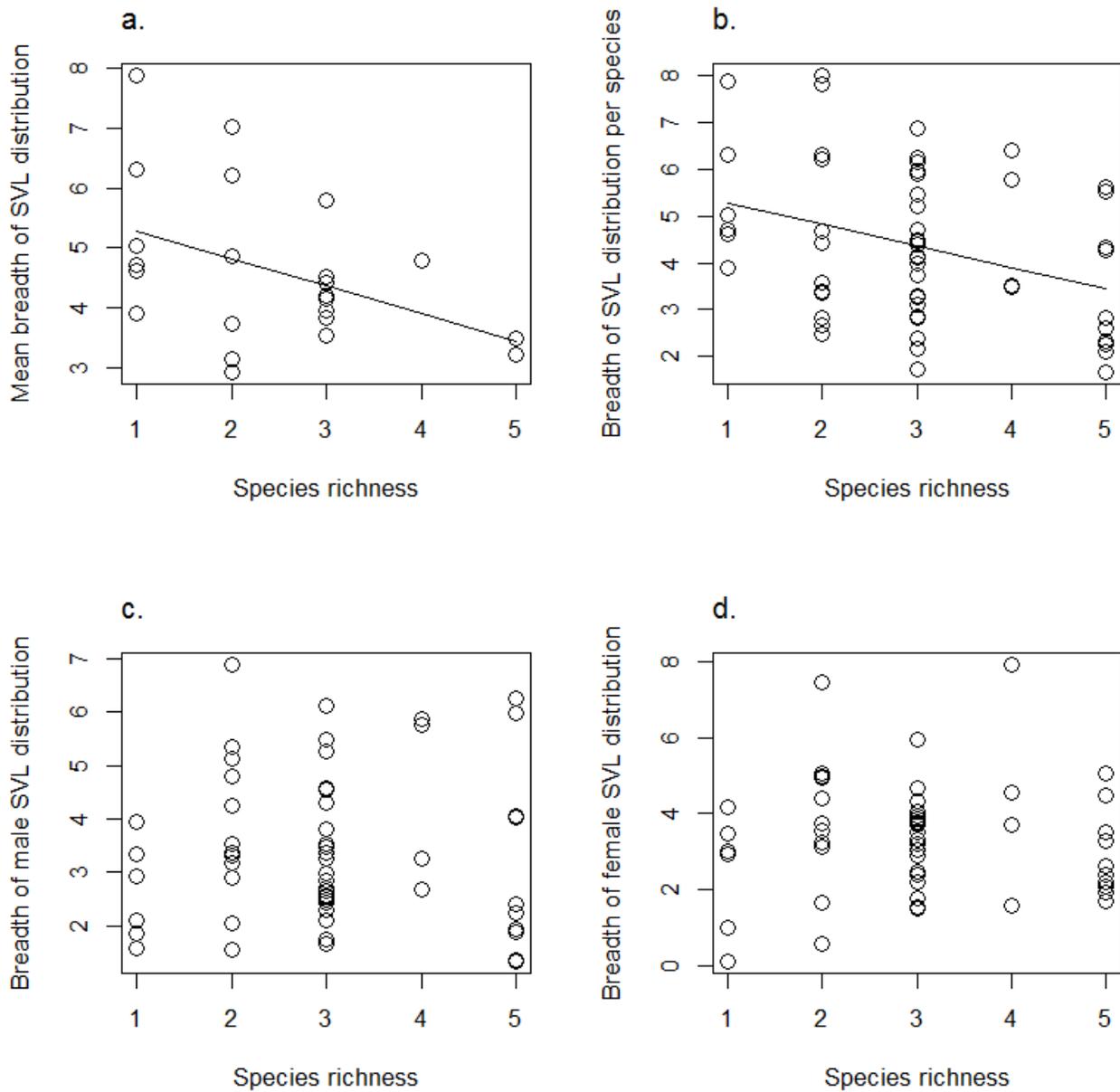
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547 **FIGURES**

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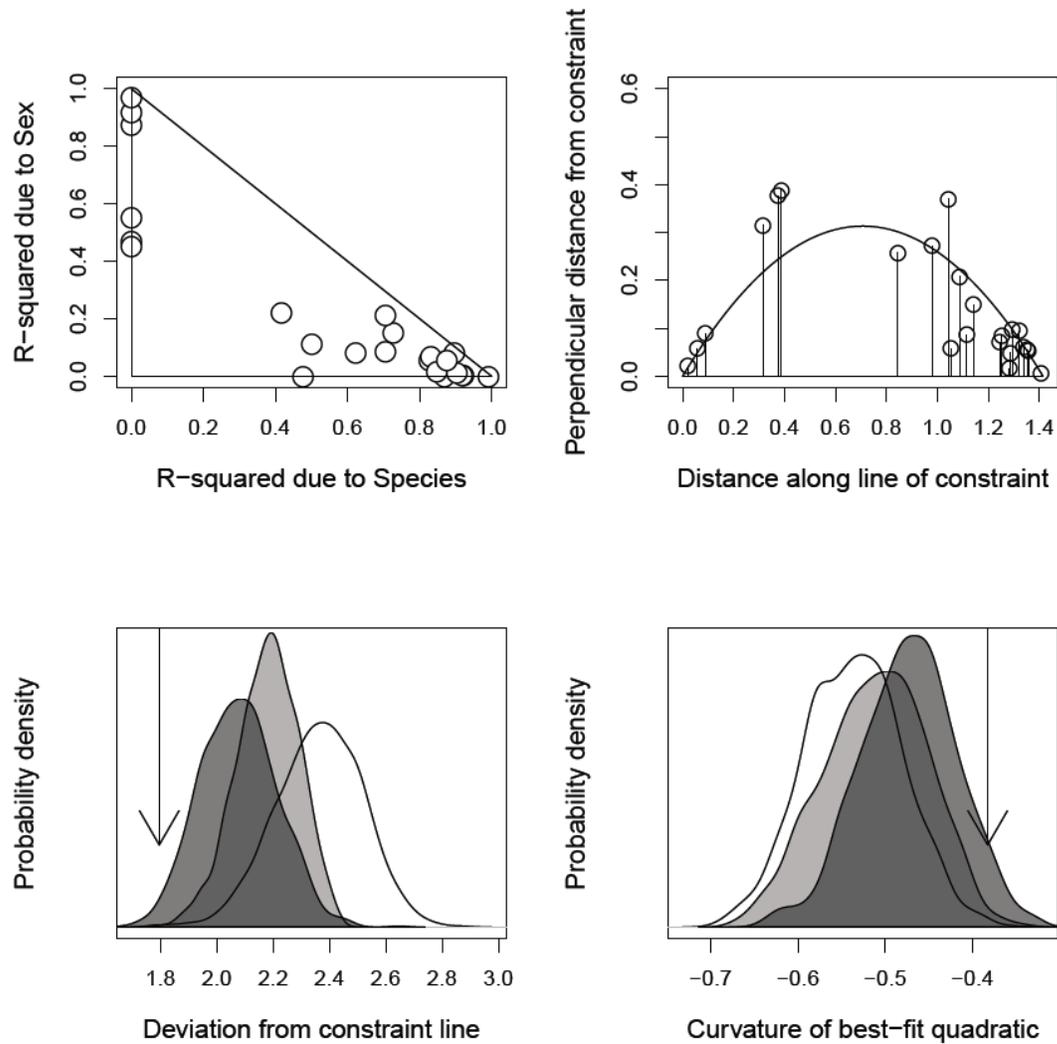
549 **Figure 1.** The relationships between sexual size dimorphism (SSD) and species-richness, described using (A)
 550 mean SSD per assemblage, or (B) per-species SSD. Correlation and mixed-model regression analyses reveal
 551 significant negative correlations compared to null expectations formed by permuting species among
 552 assemblages. Modelling with phylogenetic control yields posterior distributions of variance components and a
 553 regression slope that reveal (C) credible phylogenetic signal in the residuals of the regression of SSD against
 554 species-richness, but (D) a credibly negative relationship between SSD and richness, despite phylogenetic
 555 control.



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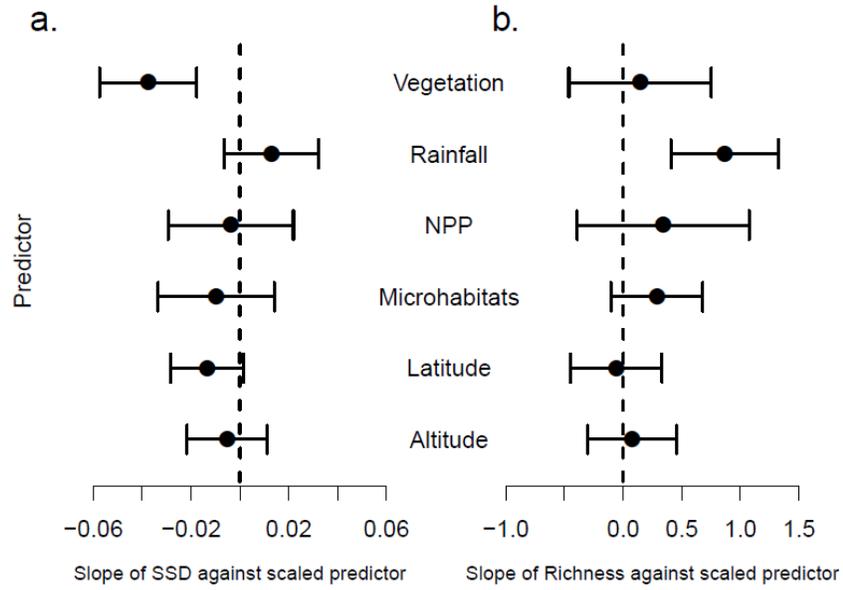
557 **Figure 2.** The relationships between species-richness and the breadth (standard deviation) of the body size
 558 distributions, either (A) per assemblage or (B) per species. Breadths correlate negatively with increasing
 559 species-richness. The body size distribution breadths of (C) males and (D) females do not correlate significantly
 560 with species-richness.

561



562

563 **Figure 3.** Deviation of each assemblage from the line of constraint that describes apportioning of all variation to
 564 between-sexes or among-species components. (A) Positions of assemblages in relation to the line constraining
 565 the proportion of variance absorbed by “sex” or “species”. (B) Conversion of these data into the distance along
 566 the line of constraint (now the x-axis) and perpendicular distance of each assemblage from this line (now the y-
 567 axis). (C) Comparison of the total squared perpendicular distances of the observed assemblages from the
 568 hypotenuse (vertical arrow), against null distributions of 10,000 permuted assemblages (white = complete shuffle
 569 of species among assemblages; light grey = constrained shuffle of sex differences; mid-grey = constrained
 570 shuffle of species differences). (D) Comparison of the curvature of a nonlinear regression of perpendicular
 571 distances from the line of constraint (vertical arrow), against null distributions of 10,000 permuted assemblages
 572 (colours as in(C)). In (C) and (D), the observed distance or curvature lies far from the main body of the null
 573 distributions, rejecting the null hypothesis in each case.



574

575

576 **Figure 4.** Model-averaged effect sizes of environmental predictors of (A) sexual size dimorphism, and (B)

577 species-richness. Mean effect sizes are presented, with 95% confidence intervals.