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

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

2

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16 **Key words:** Adaptive radiation, speciation, divergent selection, sexual dimorphism, ecological opportunity,  
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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 (Ceï, 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., Ceï, 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 2.5<sup>th</sup> 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  $R^2_{\text{sexes}}$  and  $R^2_{\text{species}}$ . 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  $R^2_{\text{sexes}}$  vs.  $R^2_{\text{species}}$  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 [ $R^2_{\text{species}}$ ,  
 237  $R^2_{\text{sexes}}$ ] 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  $R^2_{\text{sexes}}$  and  $R^2_{\text{species}}$ . 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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547 **FIGURE LEGENDS**

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

555

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

560

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

572

573 **Figure 4.** Model-averaged effect sizes of environmental predictors of (A) sexual size dimorphism, and (B)  
 574 species-richness. Mean effect sizes are presented, with 95% confidence intervals.