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

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Keywords:	Adaptive radiation, speciation, divergent selection, sexual dimorphism, ecological opportunity, niche-packing, lizards, Liolaemus

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

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Abstract

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

Location: South America

Major taxa: *Liolaemus* lizards.

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

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

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

Introduction

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

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

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

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

Materials and methods

Assemblage selection

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

Sexual size dimorphism data

Body size data were collected for all species found in the 23 studied assemblages. Snout-vent length (SVL) is the standard estimator of body size in lizards (Meiri, 2008; Pincheira-Donoso *et al.*, 2011). Hence, we used this proxy to quantify the extent of sexual size dimorphism. Given that body size in lizards follows asymptotic growth curves, the use of the largest available/known specimen or the use of the average calculated from the entire sample can overestimate or underestimate, respectively, adult body sizes (Stamps & Andrews, 1992; Brown *et al.*, 1999). Therefore, from the entire available sample of adult specimens (Pincheira-Donoso & Núñez, 2005; Pincheira-Donoso & Tregenza, 2011), we obtained the mean of the largest two-thirds of each sample per sex, per species, and per assemblage, which provides an intermediate SVL value (between the mean and maximum known for each sex), and hence, a more reliable estimate of adult body size (Losos *et al.*, 2003; Pincheira-Donoso *et al.*, 2008a). Subsequently, the degree of SSD was calculated with the formula $\ln(\mathrm{SVL}_{\mathrm{Male}}/\mathrm{SVL}_{\mathrm{Female}})$. This measure of dimorphism is intuitive and has been shown to perform with satisfactory statistical power (Smith, 1999; Fairbairn, 2007). The fundamental prediction of the theory is that the extent of sexual dimorphism varies as a function of assemblage species-richness. SSD estimates for the five *Liolaemus* species found in two assemblages (see Supplementary Table S1) were therefore calculated based on the actual specimens recorded at each specific assemblage, separately.

Relationships between SSD and species-richness

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

Controlling for phylogenetic non-independence

Recognising that observed correlations between SSD and species-richness could be due to phylogenetic patterns of SSD coupled with phylogenetically biased co-occurrences of species in assemblages, we repeated our per-species regression analyses using phylogenetic control on the residuals. There exists a well-developed phylogeny for many *Liolaemus* species (Pincheira-Donoso *et al.*, 2013a; Pincheira-Donoso *et al.*, 2015), but only half of the species in this study are represented as tips. We created a proxy phylogeny by associating unrepresented species with sister species or closest relatives that appear in the established phylogeny. This proxy phylogeny (Supplementary Figure S2; Supplementary Table S3) contains tips that can each represent multiple “real” species in our dataset. This required us to account for the influence of phylogeny using a Monte Carlo Markov Chain (MCMC) generalised linear mixed effect regression model, which considered species identity, assemblage identity and proxy phylogeny as random effects. We used the MCMCglmm package in R, and employed parameter expansion of our three random effects to ensure convergence. MCMC chains were run for 100K iterations with a burn-in of 10K and a thinning interval of 100. We report the posterior distributions of variance absorbed by phylogeny, and slope of the relationship between sexual dimorphism and species-richness.

Relationships between body size distributions and species-richness

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

Partitioning body size variation between sexes and species

The hypothesis that correlations between SSD and species-richness are driven by constraints on body size distributions (driven by size-dependent competition) predicts that, within assemblages, there should be a negative relationship between the proportion of variance in body size explained by partitioning among species and that explained by partitioning between the sexes. We expect a negative relationship between these variance components by default (because where more variance is explained by one component, less is available to be explained by the other). However, residual variance, which describes the overlap in body size distributions between sexes and among species, also contributes to total variation. If the tension between SSD and species-richness forces those ecological units into distinct portions of the body size niche dimension, then natural assemblages should lie closer to the line of perfect negative covariance than artificial assemblages made by shuffling combinations of species.

To test this prediction we performed a factorial analysis of variance in body size against sex (male or female) and species identity (one to five species), for each assemblage. We recorded the proportions of variance (R^2) explained by sexes and species, and the proportion left unexplained, then modelled the nonlinear 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 constrained to lie below the hypotenuse between [0,1] and [1,0]. Assemblages lying along the line are those in which all of the variation in body size is explained by a combination of sex- and species-identity effects. Assemblages lying closer to [0,0] are those in which body size distributions overlap considerably between sexes and among species (Figure 3). The null hypothesis for this analysis is that the natural assemblages of *Liolaemus* lie no closer to the $R^2_{\text{sexes}} + R^2_{\text{species}} = 1$ hypotenuse than random assemblages of lizard species. We tested departure from this expectation by shuffling species among assemblages 10K times and repeating the factorial ANOVA analyses for each shuffle. This approach combines the influence on niche saturation of divergence among species, and divergence between sexes. To test the influence of species divergence alone, we shuffled the size-differences among species, but constrained the size-differences between sexes to be as observed in the data. To test the influence of sexual divergence alone, we shuffled the size-differences between sexes, among species, but constrained the size-differences among species to be as observed in the data. Simulations of simplified assemblages occupying body size niches according to four simple rule-sets (a) random assembly of species and sexes; b) species occupy available niches preferentially, but sexual divergence is random; c) species occupy niches randomly, but sexual divergence occurs when niches are available; d) species and sexes both diverge into available niches) confirmed that these constrained shuffles correctly revealed niche-packing patterns due to sexual or species divergence (see supplementary material).

For the observed data and each shuffle (total shuffle; species shuffle; sex shuffle), we modelled the distance of R^2_{sexes} vs. R^2_{species} from the hypotenuse, in two ways. First, we calculated the mean deviation of perpendicular residuals from the hypotenuse. Second, recognising that shuffled assemblages with overlapping body size distributions lay closer to [0,0] than observed assemblages, and that data close to [0,0] naturally lay furthest from the hypotenuse, we used least-squares nonlinear regression to test the curvature of the quadratic fit to observed or simulated variance components that joined the constrained intercepts of [0,1] and [1,0]. The quadratic function that links x (the distance along the hypotenuse) to y (the perpendicular distance of [R^2_{species}, 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 analyses weighted the contribution of real and shuffled assemblages by the residual degrees of freedom of the associated ANOVA used to calculate R^2_{sexes} and R^2_{species}. We compared the observed outcome (mean deviation from the hypotenuse; curvature of the quadratic) to the empirical null distributions of these parameters based on our shuffles, and calculated p-values based on the quantile position of the observed parameters (Figure 3).

Sexual dimorphism: sexually or naturally selected?

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

Environmental estimators of niche space abundance

Different environments are expected to provide different diversities of potential niches to be constructed or exploited (Peterson *et al.*, 2011). Since the assemblages we sampled are widely spread along a ~3800 km latitudinal range, the availability of niche space is likely to vary across these assemblages, creating variation in their potential to host different numbers of ecological units, whether different species or divergent sexes within species. To examine this variation, we regressed SSD and species-richness against a number of environmental factors as proxies for niche diversity per assemblage. First, exclusively based on field observations, we quantified the numbers of microhabitats and the amount of vegetation available per assemblage site. Six microhabitat categories were identified in the areas occupied by *Liolaemus* (boulders, rocky ground, open ground, bushy ground, grassland, and trees) (Schulte *et al.*, 2004; Pincheira-Donoso *et al.*, 2009), which were each scored as rare (0), relatively common (0.5) or common (1). We summed these scores across microhabitat categories to yield a “microhabitats” index ranging from zero to six. Vegetation indices ranged from zero (little or no vegetation) to three (high cover of thick scrub) with intervals of 0.5. We then employed two proxies of resource abundance (Costa *et al.*, 2007; Pincheira-Donoso & Meiri, 2013; Novosolov *et al.*, 2016): mean annual precipitation (on a spatial resolution of 1/6°), assumed to be positively associated with productivity in the areas we study; and NPP, an estimate of the net amount of solar energy converted to plant organic matter through photosynthesis, measured in units of elemental carbon per year, on a spatial resolution of 1/4°. Precipitation data came from Worldclim (Hijmans *et al.*, 2005) and NPP data (log-transformed) came from Imhoff et al (2004). These climatic data were assigned to each studied community by intersecting the geographical centroids of the assemblages with the above climatic layers in ArcGIS 9.3.1. To quantify the influence of environmental factors on SSD and species-richness, we performed multiple regression analysis of mean responses per assemblage against NPP, annual precipitation, latitude, altitude, vegetation and microhabitat diversity, all scaled to have zero mean and unit variance. We used Akaike Information Criteria and Akaike model weights, and dredged the full model to determine the best model and the difference in AIC for each possible subset model using the R package ‘MuMIn’ (Barton, 2017). This full set of models was averaged, with parameters weighted by Akaike model weights, to provide means and 95% confidence intervals for the model-averaged effect sizes of each predictor. Phylogenetic control is not applicable to these analyses because we use assemblage-level, rather than species-level metrics. We then used Structural Equation Modelling (SEM), using the R package ‘sem’ (Fox *et al.*, 2017), to tease apart the relationship between environment, SSD and species richness. We used the subset of environmental predictors, identified by our multiple regressions as having significant influence on the response variables. We treated these as predictors, and considered three SEMs: first, a model in which environmental variables predicted SSD and species richness independently, but with residual covariance between these two responses; second, environmental variables predicted SSD which in turn predicted species richness; third, environmental variables predicted species richness which in turn predicted SSD. We used a combination of significance tests and AIC to compete these models, statistically.

Results

Relationship between sexual size dimorphism and species-richness

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

Correlation between breadth of body size distribution and species-richness

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

Constrained partitioning of body size variation between sexes and species

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

Is SSD generally naturally or sexually selected?

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

Environmental predictors of species-richness and SSD

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

Discussion

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

The patterns of phenotypic organization among and within species that we observe are also related to bioclimatic variation across assemblages. Species-richness increases with increasing precipitation across assemblages, presumably indirectly through its influence on vegetation and associated trophic levels that form the diet of *Liolaemus* species (greater dietary diversity facilitates higher numbers of coexisting species given the greater niche space). In contrast, while SSD is not influenced by rainfall, it increases with decreasing vegetation complexity and with increasing southerly latitude. Therefore, SSD seems to be favoured in low-complexity, low productivity environments. The latitudinal cline, however, remains unexplained. Our combined findings reveal a scenario consistent with a relationship between SSD and species-richness mediated by the environmental conditions that influence variation in available niche space per assemblage. However, despite these effects from agents of natural selection, it remains possible that sexual dimorphism has been influenced by sexual selection (see Andersson, 1994). Niche packing occurs against the backdrop of sexual selection on size dimorphism, with the potential for interactions between the two (for instance, where factors such as population density and species richness impact both ecological competition for resources and inter-male competition for mates). The action of sexual selection during the evolutionary histories of *Liolaemus* species presumably predisposes them to evolve dimorphism in the direction of males being larger than females, but our results suggest that this size difference is constrained in species-rich assemblages. We note that sexual dimorphism is greatest in habitats with low cover or complexity of vegetation, and suggest that this could be due to the importance of sexual signaling in simple habitats where visibility makes selection on display traits more intense, or due to more intense competition for scarce food resources.

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

Our surveys of sexual dimorphism and species richness did not allow us to determine cause and effect, i.e., whether the two sources of body size variation compete equally for niche space during the processes of adaptive radiation and community assembly. We suggest that variation among species is more likely to constrain the evolution of sexual dimorphism, than *vice versa*, for two main reasons. First, sexual dimorphism is evolutionarily more labile than species formation (i.e., it evolves faster, requires simpler conditions, is reversible), perhaps because it requires only a direct effect of selection on ecological traits, rather than an additional indirect effect on mating behaviour (Bolnick & Doebeli, 2003; Cooper *et al.*, 2011). Second, the magnitude of ecological divergence between the sexes is typically small compared to the magnitude of ecological divergence among coexisting species. Hence, we argue that whenever niche space has not been saturated by other species, sexual dimorphism of ecologically relevant phenotypes may evolve by natural selection through its benefits for sex-specific fitness. Such benefits may include, for example, reduced intensity of resource competition between the sexes (Shine, 1989; Bolnick & Doebeli, 2003), and relaxation of intralocus sexual conflict when intrinsic sex-specific fitness-linked roles need to evolve in different directions under the same natural selection regimes (Hedrick & Temeles, 1989; Bonduriansky & Chenoweth, 2009). Any attempt to tease apart the influence of species richness on the evolution of sexual dimorphism and/or the colonisation of dimorphic species, from the influence of sexual dimorphism on speciation and/or the colonisation of new species, would require either massive-scale experimentation, or long-term observation of evolutionary and ecological event sequences.

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

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Biosketch

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

Data Accessibility

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

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FIGURES

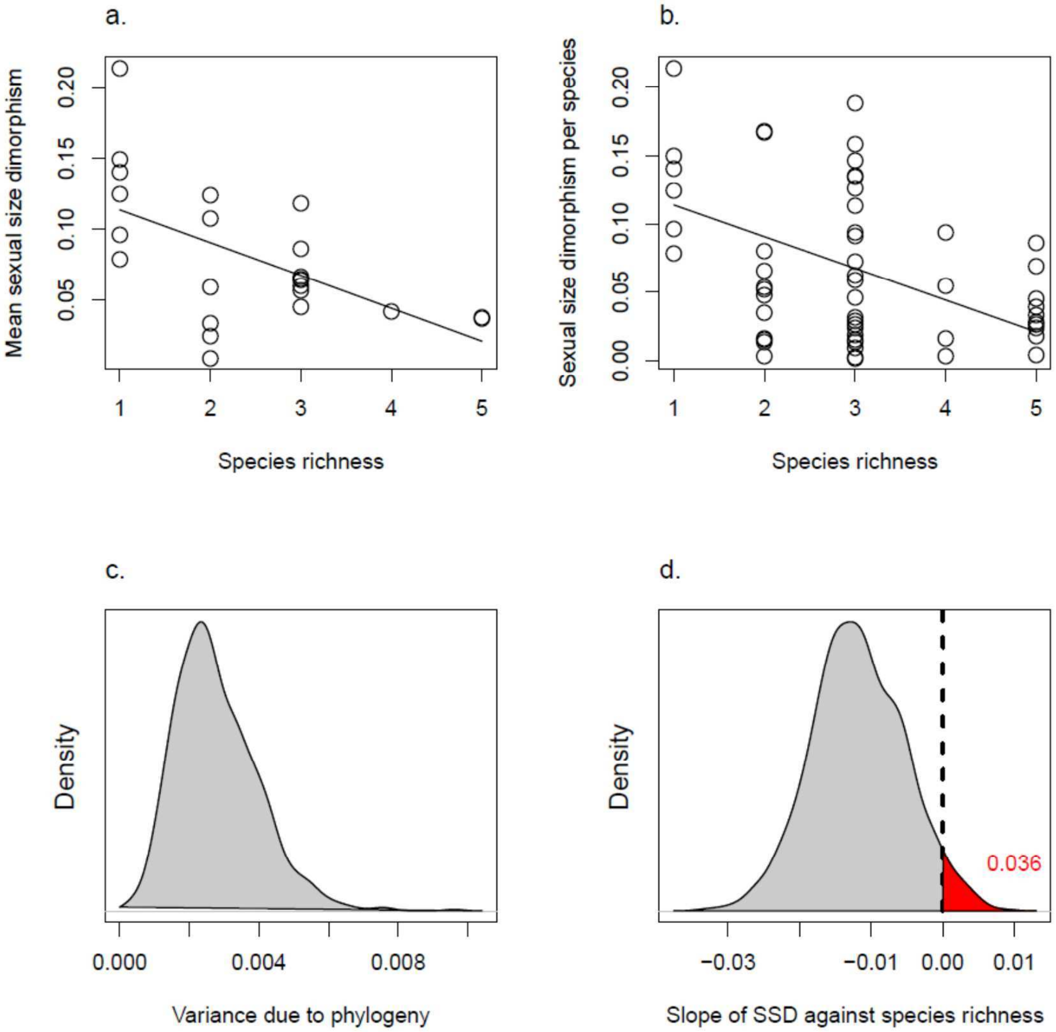

Figure 1. The relationships between sexual size dimorphism (SSD) and species-richness, described using (A) mean SSD per assemblage, or (B) per-species SSD. Correlation and mixed-model regression analyses reveal significant negative correlations compared to null expectations formed by permuting species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

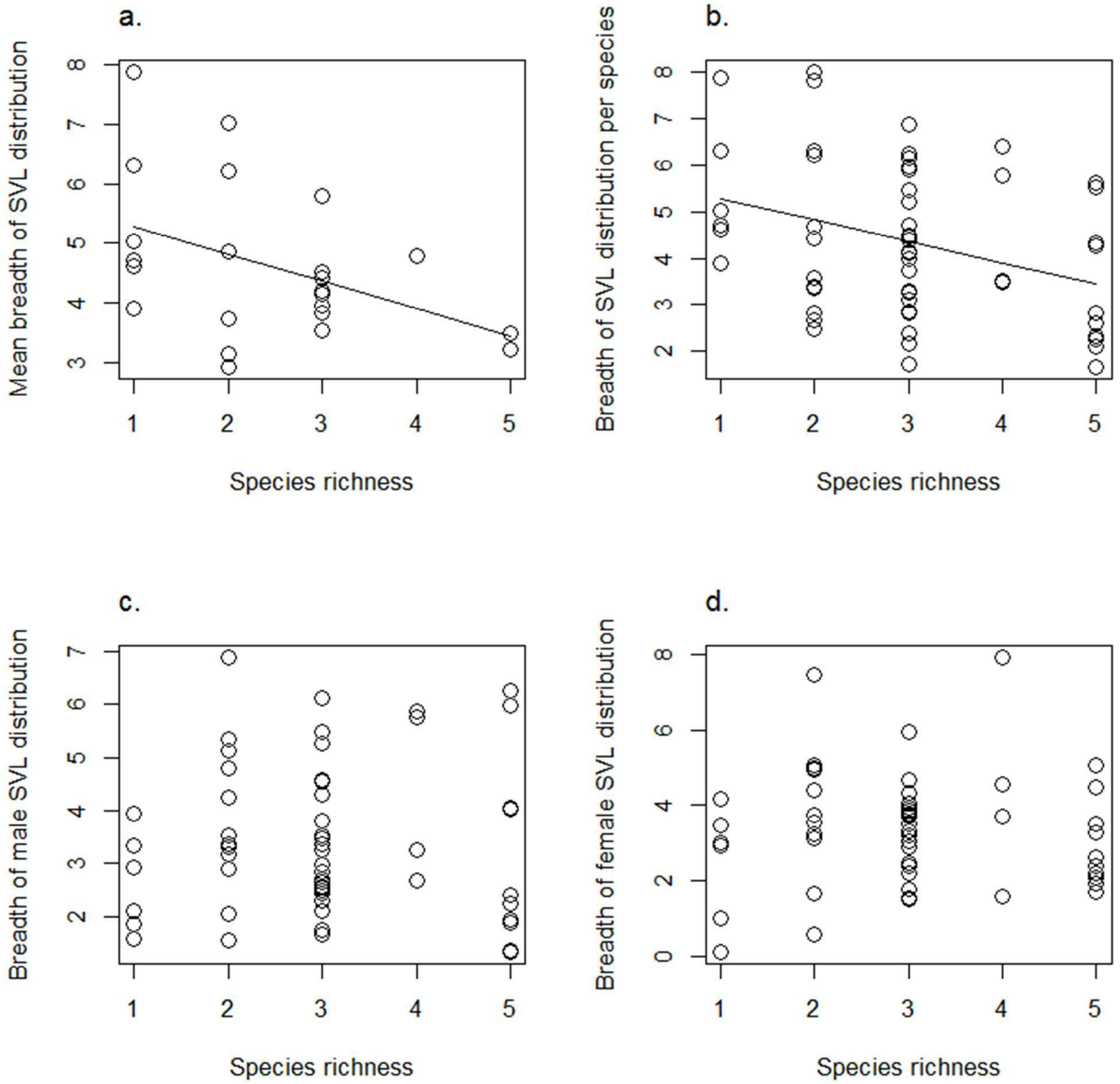

Figure 2. The relationships between species-richness and the breadth (standard deviation) of the body size distributions, either (A) per assemblage or (B) per species. Breadths correlate negatively with increasing species-richness. The body size distribution breadths of (C) males and (D) females do not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

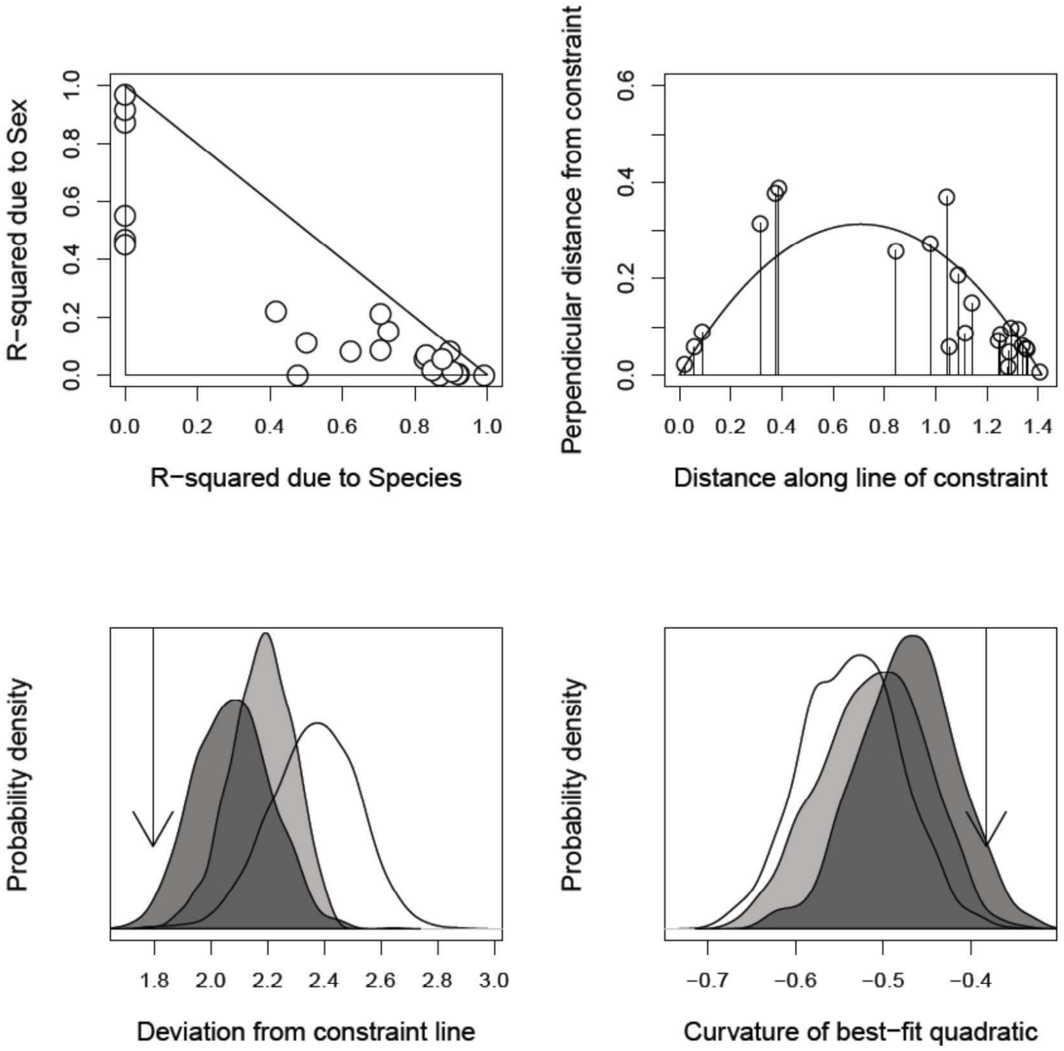

Figure 3. Deviation of each assemblage from the line of constraint that describes apportioning of all variation to between-sexes or among-species components. (A) Positions of assemblages in relation to the line constraining the proportion of variance absorbed by “sex” or “species”. (B) Conversion of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

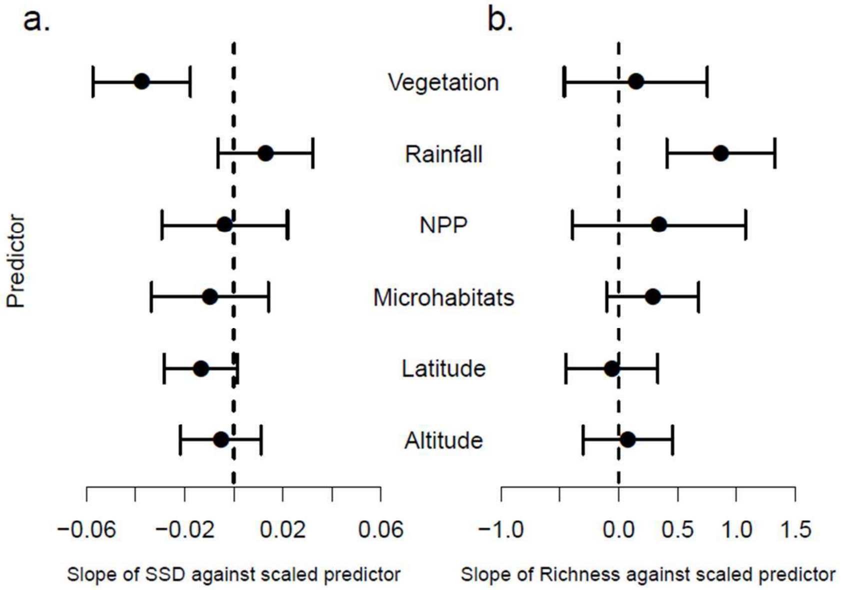

Figure 4. Model-averaged effect sizes of environmental predictors of (A) sexual size dimorphism, and (B) species-richness. Mean effect sizes are presented, with 95% confidence intervals.

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Table 1. Structured equation modelling of relationships among significant environmental predictors of SSD and species richness (latitude, annual precipitation, vegetation complexity), and response variables. Three models were fitted, describing (a) covariance between SSD and richness; (b) dependence of SSD on richness; (c) dependence of richness on SSD. Model (b) failed the goodness of fit test and was > 2 AIC units less informative than the best model. Neither of the models revealed significant dependence relationships between the response variables. Model (a) satisfied the goodness of fit test, was most informative according to AIC, and revealed significant correlation between SSD and Richness.

Model	**Term**	**Estimate (SE)**	**z-value (*P*)**	**Model fit χ^2**	***df***	***P***	**AIC**
(a) SSD & Richness covary	Latitude→SSD	-0.279 (0.12)	-2.431 (0.015)	3.83	3	0.28	15.83
	Vegetation→SSD	-0.661 (0.12)	-5.556 (<0.001)				
	Rainfall→Richness	0.875 (0.12)	7.389 (<0.001)				
	SSD↔Richness	-0.159 (0.08)	-2.063 (0.039)				
(b) SSD depends on Richness	Latitude→SSD	-0.233 (0.13)	-1.778 (0.075)	9.283	3	0.03	21.28
	Vegetation→SSD	-0.667 (0.15)	-4.507 (<0.001)				
	Rainfall→Richness	0.805 (0.13)	6.364 (<0.001)				
	Richness→SSD	-0.057 (0.14)	-0.407 (0.684)				
(c) Richness depends on SSD	Latitude→SSD	-0.236 (0.13)	-1.808 (0.071)	5.644	3	0.13	17.64
	Vegetation→SSD	-0.703 (0.13)	-5.378 (<0.001)				
	Rainfall→Richness	0.685 (0.14)	4.744 (<0.001)				
	SSD → Richness	-0.265 (0.14)	-1.833 (0.067)				

SUPPLEMENTARY INFORMATION

SUPPLEMENTARY ANALYSES AND TABLES

Supplementary Table S1. Summary of data used in this study, indicating the number of species in each assemblage, the body size (SVL) per sex, and environmental predictors obtained from centroid geographic location of each assemblage. See methods for details.

	Species Richness			SVL				
Assemblage	**Nº**	**Species**	***N***	**Males**	**Females**	**Centroid Geographic Location**	**log(NPP)**	**Precipitation**
Arica	1	*L. poconchilensis*	6	59.39	47.97	18º29’S, 70º07’W	10.570	7
Iquique	1	*L. stolzmanni*	7	59.17	50.92	20º13’S, 70º01’W	10.279	1
Quisquiro	1	*L. andinus*	43	67.52	62.38	23º11’S, 67º17’W	10.833	62
Isla Locos	1	*L. zapallarensis*	–[a]	107.5	93.30	32º07’S, 71º31’W	10.690	250
Antofagasta	1	*L. hellmichi*	29	57.17	50.45	23º29’S, 70º33’W	10.156	3
Pantanillo	1	*L. rosenmanni*	44	74.09	67.28	27º26’S, 69º02’W	10.640	78
Puritama	2	*L. barbarae*	11	49.40	46.23	22º49’S, 68º07’W	10.819	36
		L. puritamensis	11	97.23	92.12			
Calama	2	*L. paulinae*	18	53.35	52.57	22º27’S, 68º50’W	10.603	26
		L. torresi	8	56.12	58.03			
Baños El Toro	2	*L. lorenzmuelleri*	13	95.16	80.39	29º49’S, 70º01’W	10.610	142
		L. robertoi	26	63.66	58.71			
La Ola	2	*L. isabelae*	14	78.96	66.79	26º26’S, 69º06’W	10.421	33
		L. patriciaiturrae	22	88.33	84.18			
Rio Gallegos	2	*L. magellanicus*	36	59.62	59.85	51º49’S, 69º21’W	11.032	236
		L. sarmientoi	47	86.19	84.83			
Meseta Aguila-Asador	2	*L. gallardoi*	29	89.25	84.69	47º56’S, 71º33’W	10.909	250
		L. hatcheri	32	63.05	64.11			
El Morado	3	*L. moradoensis*	20	59.18	59.02	33º47’S, 70º02’W	10.842	564
		L. nigroviridis	47	69.58	57.60			
		L. valdesianus	25	88.79	89.08			
Chungara	3	*L. alticolor*	34	50.06	47.79	18º12’S, 69º12’W	11.113	306
		L. jamesi	38	93.12	87.45			
		L. pleopholis	18	75.37	70.05			
Barros Arana	3	*L. audituvelatus*	–	ND	ND	22º39’S, 68º28’W	10.764	29
		L. constanzae	60	67.87	60.55			
		L. foxi	11	80.74	76.09			
Farellones	3	*L. bellii*	99	74.66	72.85	33º20’S, 70º17’W	11.135	504
		L. leopardinus	23	88.48	85.90			
		L. nigroviridis	49	73.69	63.62			
Cerro Ramon	3	*L. cf. bellii*	17	63.22	61.56	33º29’S, 70º26’W	11.135	537

		L. ramonensis	22	88.96	89.87			
		L. nigroviridis	27	73.47	62.67			
Diego de Almagro	3	*L. atacamensis*	40	75.15	65.66	26º23'S, 70º02'W	10.504	13
		L. manueli	18	54.57	49.81			
		L. velosoi	48	51.90	46.83			
Salar de Atacama	3	*L. audituvelatus*	10[b]	55.05	56.13	23º02'S, 68º07'W	10.763	47
		L. constanzae	84	68.91	60.18			
		L. fabiani	28	79.89	78.64			
Meseta Lago Buenos Aires	3	*L. archeforus*	36	85.29	84.08	47º03'S, 71º02'W	10.837	187
		L. lineomaculatus	32	61.29	55.71			
		L. silvanae	33	75.37	72.99			
Termas del Flaco	4	*L. chiliensis*	31	87.52	88.58	34º56'S, 70º27'W	10.819	762
		L. curicensis	42	61.59	56.06			
		L. curis	33	91.45	86.37			
		L. schroederi	23	59.99	61.60			
Copahue	5	*L. cf. buergeri*	25	93.83	90.95	37º48'S, 71º05'W	11.401	1044
		L. coeruleus	33	63.13	61.03			
		L. elongatus	19	69.84	67.13			
		L. neuquensis	28	61.49	61.21			
		L. tregenzai	15	83.97	76.98			
Concepcion	5	*L. chiliensis*	32	81.83	82.77	36º48'S, 72º58'W	11.834	1325
		L. cyanogaster	29	64.06	64.83			
		L. lemniscatus	60	47.84	45.97			
		L. schroederi	35	56.39	60.79			
		L. tenuis	101	56.05	54.62			

[a] SSD obtained from male and female averages calculated based on previously obtained averages for each sex.

[b] SSD calculated previously based on this sample but only the averages available now

Supplementary Analysis S2 and Table S2

Contribution of species- and sexual-divergence to niche packing: a simulation study.

In our analyses, we consider the influence of ecological opportunity on size divergence among resident species, and sexes of those species, in natural assemblages. The argument is that species will tend to coexist when they occupy distinct portions of the body size niche dimension, and sexes will tend to diverge into available niche space. This sets up a tension between species richness and sexual dimorphism, since the two compete for available niche space.

We provide an analysis that partitions variation in body size into three components: among species, between sexes, and residual variation. The relative magnitudes of these three components describe the extent to which species and sexes occupy distinct, non-overlapping portions of the body size niche dimension. The analysis suffers a triangular constraint such that the R^2 values for species, sexes and residuals must each be positive and must sum to 1. To test whether the observed assemblages are structured by niche-packing processes, we shuffled species among assemblages and compared how close to the line of perfect constraint lay the observed assemblages, compared to the shuffled assemblages. However, the significance of this permutation test could be driven by either species differences or sex differences or both. The complete shuffle demonstrated that the observed assemblages were clearly niche-packed, but does not tease apart the relative influence of divergence among species and between sexes.

To overcome this, and therefore to ask whether sexual dimorphism and species differences both exploit ecological opportunity, we performed constrained permutation tests. To test the influence of sexual dimorphism, we constrained the species-level body size differences in each assemblage to be as observed, but shuffled the differences between the sexes, then compared the observed assemblages to the null distribution of shuffled assemblages. To test the influence of species differences, we constrained the sexual divergence of species in each assemblage to be as observed, but shuffled the differences between the species, then compared the observed assemblages to the null distribution of shuffled assemblages. The structured shuffles were achieved by fitting a GLM of body size against species identity and sex for each assemblage, then shuffling the sex-differences or species-differences among assemblages. The total shuffle was achieved by shuffling the “assemblage” identity among species.

This is a complicated set of shuffles that deserves a demonstration of statistical rigour and power. Any change to the R^2 explained by species can cause a change in both the R^2 for sexes and the residual R^2, thanks to the triangular constraint.

Consider a simple environment in which body sizes can range between 1 and 6 size units. We populate replicated environments with assemblages of species richness 1-5 (five replicates of each richness). We draw samples of body sizes for each sex of each species, from a Gaussian distribution with standard deviation 0.3 and mean determined by the integer position of each sex in each species along the body size dimension. We assemble the assemblages according to four rule-sets:

a) Random assembly. Here, mean species body sizes occupy the niche dimension at random integers, and sexes diverge by 0 or 1 unit of body size chosen at random. There is no niche-packing process, and we expect to observe no difference between observed and shuffled assemblages.

b) Species and sexes diverge if niche space is available. Here, species assemble into available body size integers, and sexes diverge if neighbouring body size integers are unoccupied. If neighbouring body size regions are already occupied, the sexes do not diverge. If no body size regions are available, species or sexes overlap in body size. We expect to observe niche-packing from our total shuffle, from the sex-shuffle, and from the species-shuffle.

c) Species assemble into available niche space but sexual dimorphism is random. Here, species are placed at mean body sizes described by vacant body size integers, if available. Sexual divergence is then “added” as a random draw from a Uniform distribution with limits [0,1]. We are obliged to avoid the bimodal option for sexual divergence here, because it creates biases in the single-species assemblages. We expect to observe niche-packing in the species-shuffle, but not in the sex-shuffle. If species-level niche packing is sufficiently strong, then the total shuffle should reveal niche-packing.

d) Species assemble at random but sexual dimorphism only occurs if niche space is available. Here, species’ mean body sizes are placed at random integers. Sexual divergence of 1 unit is added if the neighbouring body size integer is unoccupied. We expect to observe niche-packing in the sex-shuffle but not in the species-shuffle. If the sex-level niche packing is sufficiently strong, then the total shuffle should reveal niche-packing.

We assembled groups of 25 assemblages (5 replicates each of species richness 1-5), for each of these assembly rule-sets, and applied our nonlinear least-squares analysis of deviation from the constraint hypotenuse (see Methods in the main text). We then performed the total-shuffle, species-shuffle and sex-shuffle to the simulated assemblages, and compared the curvature parameter of the "observed" simulated assemblages to the respective null distributions. The outcomes are described in Table S2 below, and confirm that the constrained shuffles detect the correct sources of niche-packing. We have performed this entire analysis for several complete sets of simulated assemblages. There is inevitably some variation among simulated outcomes, but when niche-packing is detectable, it is always due to the correct process (sexual divergence or species divergence or both). If niche-packing is not detected as significant (due to the simulation outcome), the correct process is always closer to the line of constraint. For example in Table S2, the packing of niches by sexes reveals a near-significant *P*-value for the sex-shuffle, a much larger *P*-value (>> 0.5) for species-level niche packing, and the overall outcome is *P* = 0.04 for the total shuffle. The key outcome from this process is that it strongly suggests that the very clear niche packing described by our total-shuffle is the result of packing both due to divergence among species and divergence between sexes within species.

Supplementary Table S2. Tests of niche-packing signal due to divergence among species, divergence between sexes, and both, as detected by shuffled species differences, shuffled sex differences, and total shuffles. Empirical *P*-values report the quantile position of the observed distance from the line of perfect niche-packing constraint, for each shuffling algorithm applied to assemblages simulated using each rule set. We embolden the empirical *P*-values that are <0.1 for each rule-set: these tally with those predicted to be significant. Outcome from the *real Liolaemus* data is appended in final row.

Rule Set	Total Shuffle	Species Shuffle	Sex Shuffle
Random assembly	*P* = 0.34	*P* = 0.38	*P* = 0.59
Sexes and species pack niches	***P* = 0.05**	***P* = 0.02**	***P* = 0.04**
Random species, sexes pack niches	***P* = 0.06**	*P* = 0.32	***P* = 0.04**
Random sexes, species pack niches	***P* < 0.01**	***P* = 0.02**	*P* = 0.78
Liolaemus	***P* = 0.001**	***P* = 0.049**	***P* = 0.01**

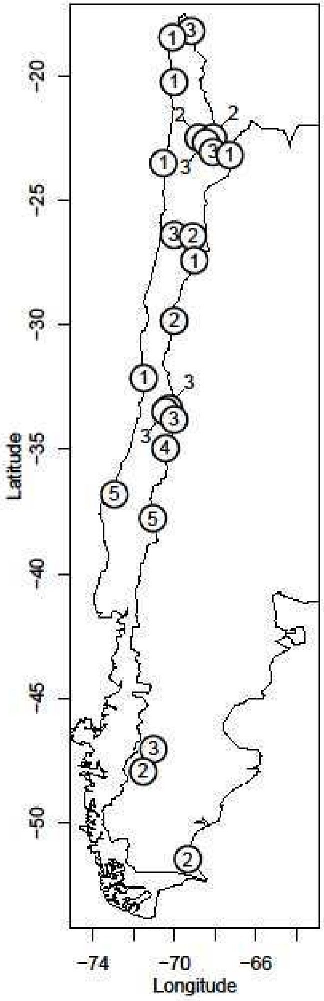
Supplementary Table S3. Proxy species used for phylogenetic analysis of relationships between sexual size dimorphism and species richness. All species are in the Genus *Liolaemus*. Left column lists all the constituent members of the assemblages used in these analyses. Right column lists their closest relatives that exist in the phylogeny used for analysis (from Pincheira-Donoso et al., 2015, BMC Evolutionary Biology, 15: 153). For phylogenetic regression, each species was associated with this closest relative species, to allow detection of phylogenetic signal among residuals.

Species	**Proxy relative in phylogeny**
Liolaemus poconchilensis	*Liolaemus reichei*
Liolaemus reichei	*Liolaemus reichei*
Liolaemus andinus	*Liolaemus molinai*
Liolaemus sieversi	*Liolaemus zapallarensis*
Liolaemus hellmichi	*Liolaemus platei*
Liolaemus rosenmanni	*Liolaemus fabiani*
Liolaemus barbarae	*Liolaemus puna*
Liolaemus puritamensis	*Liolaemus dorbignyi*
Liolaemus paulinae	*Liolaemus paulinae*
Liolaemus torresi	*Liolaemus fabiani*
Liolaemus lorenzmuelleri	*Liolaemus nigroviridis*
Liolaemus robertoi	*Liolaemus vallecurensis*
Liolaemus isabelae	*Liolaemus atacamensis*
Liolaemus patriciaiturrae	*Liolaemus molinai*
Liolaemus moradoensis	*Liolaemus bellii*
Liolaemus nigroviridis	*Liolaemus nigroviridis*
Liolaemus valdesianus	*Liolaemus leopardinus*
Liolaemus alticolor	*Liolaemus walkeri*
Liolaemus jamesi	*Liolaemus molinai*
Liolaemus pleopholis	*Liolaemus orientalis*
Liolaemus audituvelatus	*Liolaemus audituvelatus*
Liolaemus constanzae	*Liolaemus nigroviridis*
Liolaemus foxi	*Liolaemus multicolor*
Liolaemus bellii	*Liolaemus bellii*

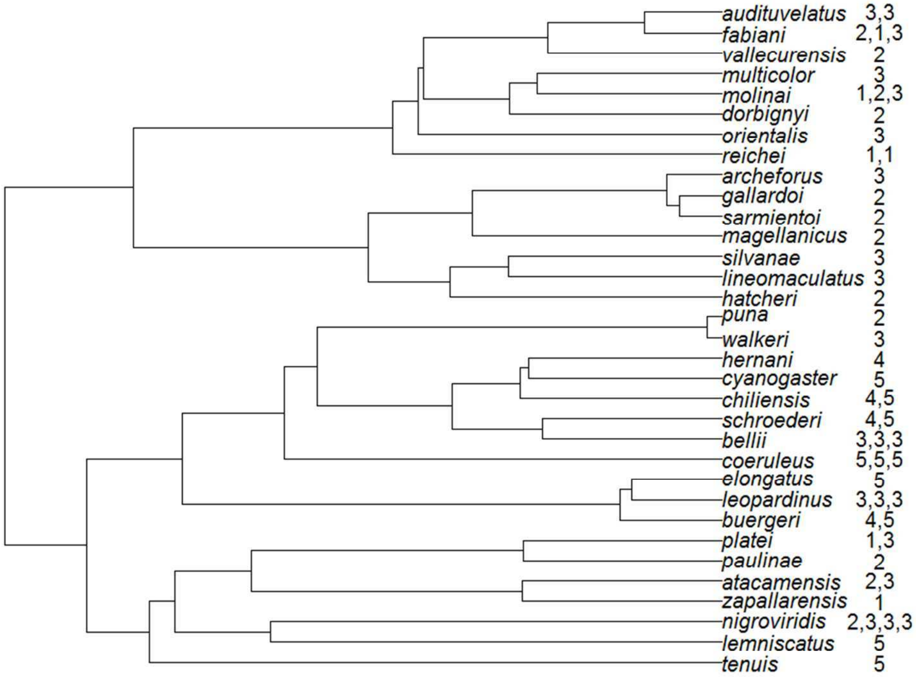
Liolaemus leopardinus	*Liolaemus leopardinus*
Liolaemus cf. bellii	*Liolaemus bellii*
Liolaemus ramonensis	*Liolaemus leopardinus*
Liolaemus atacamensis	*Liolaemus atacamensis*
Liolaemus manueli	*Liolaemus audituvelatus*
Liolaemus velosoi	*Liolaemus platei*
Liolaemus fabiani	*Liolaemus fabiani*
Liolaemus chiliensis	*Liolaemus chiliensis*
Liolaemus curicensis	*Liolaemus hernani*
Liolaemus curis	*Liolaemus cf. buergeri*
Liolaemus schroederi	*Liolaemus schroederi*
Liolaemus cyanogaster	*Liolaemus cyanogaster*
Liolaemus lemniscatus	*Liolaemus lemniscatus*
Liolaemus tenuis	*Liolaemus tenuis*
Liolaemus magellanicus	*Liolaemus magellanicus*
Liolaemus sarmientoi	*Liolaemus sarmientoi*
Liolaemus gallardoi	*Liolaemus gallardoi*
Liolaemus periglacialis	*Liolaemus hatcheri*
Liolaemus archeforus	*Liolaemus archeforus*
Liolaemus lineomaculatus	*Liolaemus lineomaculatus*
Liolaemus silvanae	*Liolaemus silvanae*
Liolaemus cf. buergeri	*Liolaemus cf. buergeri*
Liolaemus coeruleus	*Liolaemus coeruleus*
Liolaemus elongatus	*Liolaemus elongatus*
Liolaemus neuquensis	*Liolaemus coeruleus*
Liolaemus tregenzai	*Liolaemus elongatus*

SUPPLEMENTARY FIGURES

Supplementary Figure S1. Map of South America west of the Andes, showing centroids of the range of each *Liolaemus* assemblage in this study, with species richness of each assemblage labelled. The map was created using ArcGIS v9.3.1 (https://www.arcgis.com/).



Supplementary Figure S2. Proxy phylogeny for the *Liolaemus* species in this study. This phylogenetic tree is a subset of that published in Pincheira-Donoso et al (2013b; see main text for References) and shows tips representing either the species measured here, or closest relatives of these species. Numbers next to each tip of the phylogeny are the species richnesses of the assemblages of which the tip species is a member (or the closest relative of a member). Visual inspection suggests that members of species-poor and species-rich assemblages are clustered phylogenetically. This is confirmed by MCMCglmm models (see main text).



Supplementary Figure S3. Empirical probability density functions of body size distributions per-sex and per-species, in each of the *Liolaemus* assemblages studied. Each sub-plot refers to a different assemblage (named geographically). Each species is coloured differently, while solid lines represent male and dashed lines female body sizes.