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²⁶ **Data Archiving:** Data are available on DRYAD (doi:10.5061/dryad.xwdbrv1f6 (Tejero-Cicuéndez et al.
²⁷ 2021b)). R-scripts are available at **XXX**.

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³¹ **Abstract**

³² asdf

33 Introduction

34 some general paragraph on the evolution of phenotypic diversity

35
36 when organisms colonize new and unique habitats, they are subjected to novel ecological selection pressures
37 in those habitats. Often these selective pressures elicit changes in body form, as organisms adapt to their
38 new habitats (examples: some comment on ecomorphs, etc.). . . . leads to so-called ecomorphs, with such
39 well known examples in Anolis lizards, cichlid fishes, etc. It follows that . . . Some comment on the fact that
40 clades living in diverse ecological conditions often display greater diversity in form and function (REFS).

41 However, while the above patterns have been well documented in a variety of vertebrate taxa, what remains
42 less known is how allometry plays a role in this phenotypic diversification. We know that XYZPDQ (about
43 allometry). Then links to diversity..

44 The Afro-Arabian geckos in the genus *Pristurus* afford the opportunity to elucidate the interdigitating effects
45 of allometry and habitat specialization on clade-level patterns of phenotypic diversity. Prior work on this
46 system (Tejero-Cicuéndez et al. 2021a) has revealed that . . . (sentence or 2 about your prior study, getting
47 to diversity and . . . Importantly, . . . something about habitat. . . . What remains unexamined however, is
48 XYZPDQ. . .

49 In this study, we . . .

50 Materials and Methods

51 Data

52 For this study, we combined phenotypic, phylogenetic, and ecological data to evaluate macroevolutionary
53 trends in allometry in *Pristurus* geckos, and to discern the extent to which those patterns differed across
54 species occupying distinct ecological habitats. The data were obtained from our prior work on this system
55 (Tejero-Cicuéndez et al. 2021a, 2022), and are briefly described here. First we used a time-dated, molecular
56 phylogeny that included all members of the genus *Pristurus*, including several currently undescribed taxa.
57 The tree was estimated in a Bayesian framework, using five mitochondrial markers, six nuclear markers, and
58 21 calibration points (for details see Tejero-Cicuéndez et al. 2022). Next we categorized each species as
59 belonging to one of three ecological groups (ground, rock, or tree), based on descriptions of habitat use found
60 in the literature (see Tejero-Cicuéndez et al. 2021a). Finally, we obtained a phenotypic data set containing
61 body size (snout-vent length: SVL) and eight linear measurements (Figure 1) that described overall body

form: trunk length (TrL), head length (HL), head width (HW), head height (HH), humerus length (Lhu), ulna length (Lun), femur length (Lfe), and tibia length (Ltb) (Tejero-Cicuéndez et al. 2021a). We restricted our study to those species represented by five or more individuals; resulting in a dataset of 687 individuals from 25 species (individuals per species: $\mu = 27$; min = 9, max = 56). Species in the phenotypic dataset were then matched to the phylogeny, which was subsequently pruned to arrive at the final topology. All measurements were log-transformed prior to statistical analyses. Additional details regarding data collection and formal descriptions of each linear measurement may be found in the original sources (see Tejero-Cicuéndez et al. 2021a, 2022). The data are found on DRYAD: <https://doi.org/10.5061/dryad.xwdbvr1f6> (Tejero-Cicuéndez et al. 2021b).

Statistical and Comparative Analyses

We conducted a series of analyses to interrogate allometric trends and macroevolutionary changes in allometry, relative to diversification in body form. First, to determine whether allometric trends in body form differed across habitat groups, we performed a multivariate analysis of covariance, with body size (*SVL*), *habitat*, and *SVL* \times *habitat* as model effects. Significance was evaluated using 999 iterations of a permutation procedure, where residuals from a reduced model were randomly permuted in each permutation (RRPP), model statistics were recalculated, and used to generate empirical null sampling distributions to evaluate the observed test statistics (following Freedman and Lane 1983; Collyer and Adams 2007; Collyer et al. 2015). Next we compared the multivariate allometric vectors for each habitat group by calculating pairwise differences in their angular direction in morphospace, and evaluating these relative to empirical sampling distributions obtained through RRPP (Collyer and Adams 2007; Adams and Collyer 2009; Collyer and Adams 2013). We then visualized patterns of multivariate allometry relative to body size via regression scores (Drake and Klingenberg 2008) and predicted lines (Adams and Nistri 2010), based on the coefficients and fitted values from the linear model described above.

Second, we examined changes in allometric trends across the phylogeny, treating the head dimensions and limb dimensions separately. Because both the head and limb data were multivariate, we accomplished this by first performing a partial least squares analysis (Rohlf and Corti 2000) of the head traits versus SVL, and the limb traits versus SVL, and retaining the PLS scores for each individual from the first dimension of this analysis. Species-specific slopes describing the extent of head and limb allometry within each species were then obtained from an analysis of covariance modeled as: $PLS1_{head} \sim SVL * species$ and $PLS1_{limb} \sim SVL * species$ respectively. Species' slopes were then mapped on the phylogeny of *Pristurus*

using a Brownian motion model of evolution, to qualitatively evaluate shifts in allometry across species (for a similar approach see Adams and Nistri 2010).

Finally, to relate within-species allometric trends with patterns of phenotypic diversification in the group we generated a phylomorphospace, based on the size-standardized species means obtained from a phylogenetic regression (see Tejero-Cicuéndez et al. 2021a). Here, phenotypic similarities among species, relative to their phylogenetic relationships and habitat affiliations, were observed. All analyses were conducted in R 4.2.1 (R Core Team 2022), using RRPP version 1.3.1 (Collyer and Adams 2018; Collyer and Adams 2022), and scripts written by the authors (available at **XXX**).

Results

Our analyses revealed significant differences in the allometry of body form among *Pristurus* that utilized distinct habitats (Table 1). Further, comparisons of multivariate allometric vectors identified that ground-dwelling *Pristurus* displayed a distinct allometric trend as compared with *Pristurus* occupying both the rock and tree habitats (Table 2). A visualization of multivariate allometric trends (Fig. 2) confirmed these statistical findings, and indicated that the allometric trajectory in rock-dwelling animals was more extreme as compared with either ground or tree-dwelling *Pristurus*. Inspection of individual regression coefficients for each trait (Supplemental Information) further corroborated this, revealing steeper allometric coefficients for all head and limb traits in ground-dwelling *Pristurus* as compared with rock and tree-dwelling taxa. Overall, these findings revealed that larger individuals of ground-dwelling *Pristurus* species displayed proportionately larger heads and limbs, as compared with large individuals in taxa utilizing other habitat types.

Ground: head and body dimensions are more positively allometric (relative to SVL) than in rock/tree groups, and whereas allometric coefficients more similar in rock & tree.

Formally evaluated using PLS: confirming When mapped on the phylogeny (.) Here traitgrams (by SVL) elucidated that heads more strongly allometric in XXX, implying that larger individuals of these species display proportionately larger heads relative to the ‘typical’ trend in the genus. By contrast, . . . less strong (negative?) allometry
steeper/shallower slopes? resulting in . . .

¹²² **Careful! use steeper slope, not positive/negative.

¹²³ When viewed in light of phylomorphospace. . . .

¹²⁴ **Discussion**

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Table 1: Multivariate analysis of covariance describing variation in body form in extitPristurus.

	Df	SS	MS	Rsqr	F	Z	Pr(>F)
svl	1	516.036559	516.0365588	0.9203096	10188.69842	9.490057	0.001
habitat	2	6.218510	3.1092552	0.0110902	61.38957	9.322480	0.001
svl:habitat	2	3.974307	1.9871536	0.0070879	39.23464	7.077264	0.001
Residuals	681	34.491245	0.0506479	0.0615124			
Total	686	560.720622					

Table 2: Pairwise comparisons of multivariate allometry vectors. Effect sizes ($Z_{\theta_{12}}$) based on pairwise differences in angular direction are below the diagonal, and their corresponding significance levels are above diagonal. Significant values in bold.

	Ground	Rock	Tree
Ground	0	0.001	0.001
Rock	6.872	0	0.261
Tree	3.657	0.649	0

Figures

Figure 1. Linear Measurements used in this study. SVL = snout-vent length, TL = trunk length, HL = head length, HW = head width, HH = head height, Lhu = humerus length, Lun = ulna length, Lfe = femur length, Ltb = tibia length (for details see Tejero-Cicuéndez et al. 2021a).

Figure 2. Plot of regression scores and predicted lines representing the relationship between linear body measurements and size (SVL). Individuals are colored by habitat use: rock (beige), ground (dark purple), and tree (magenta).

Figure 3. Traitgrams showing the evolution of body size (SVL) through time based on the phylogenetic tree of *Pristurus*. Colors represent an evolutionary mapping of regression slopes describing the relationship of (A) head morphology versus body size, and (B) limb proportions versus body size (see text for descriptions). Species names are colored by habitat use: rock (beige), ground (dark purple), and tree (magenta).

Figure 4. Phylomorphospace of *Pristurus*, based on residuals from a phylogenetic regression of body measurements on size (SVL). Species means are colored by habitat use: rock (beige), ground (dark purple), and tree (magenta). Large and small rock-dwelling and ground-dwelling are highlighted with darker colors to highlight their differentiation and relative positions in morphospace.

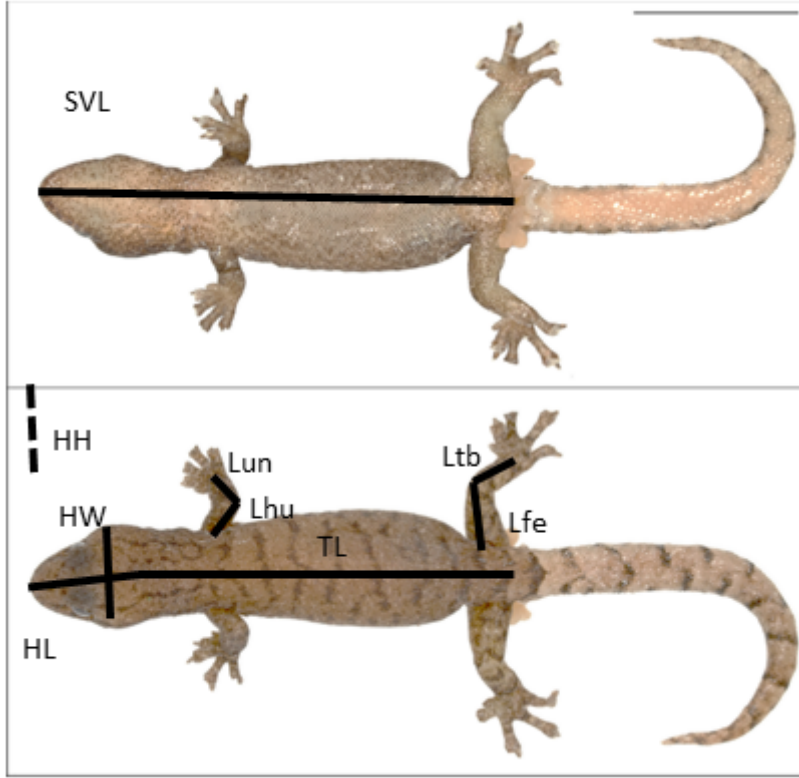


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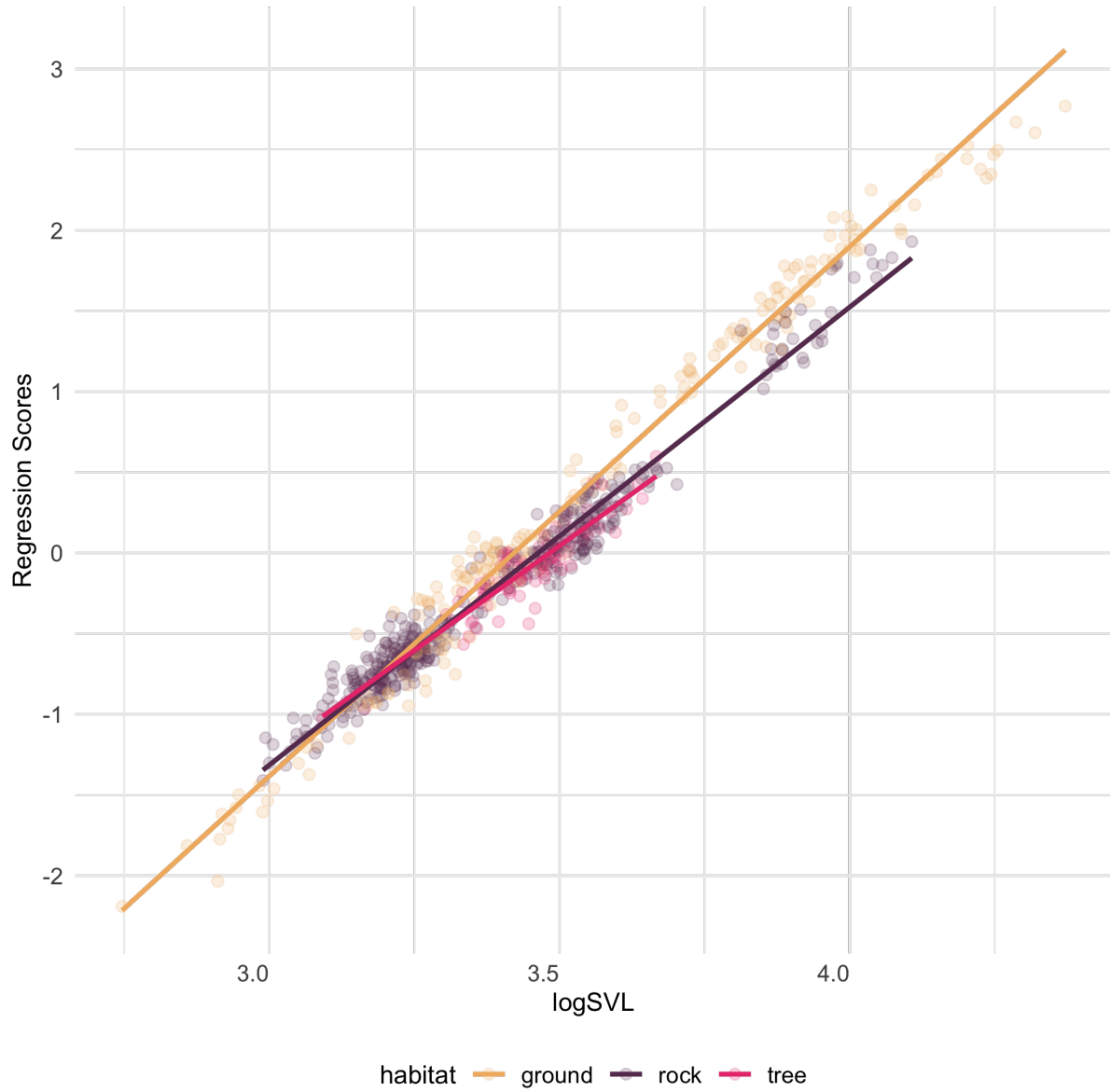


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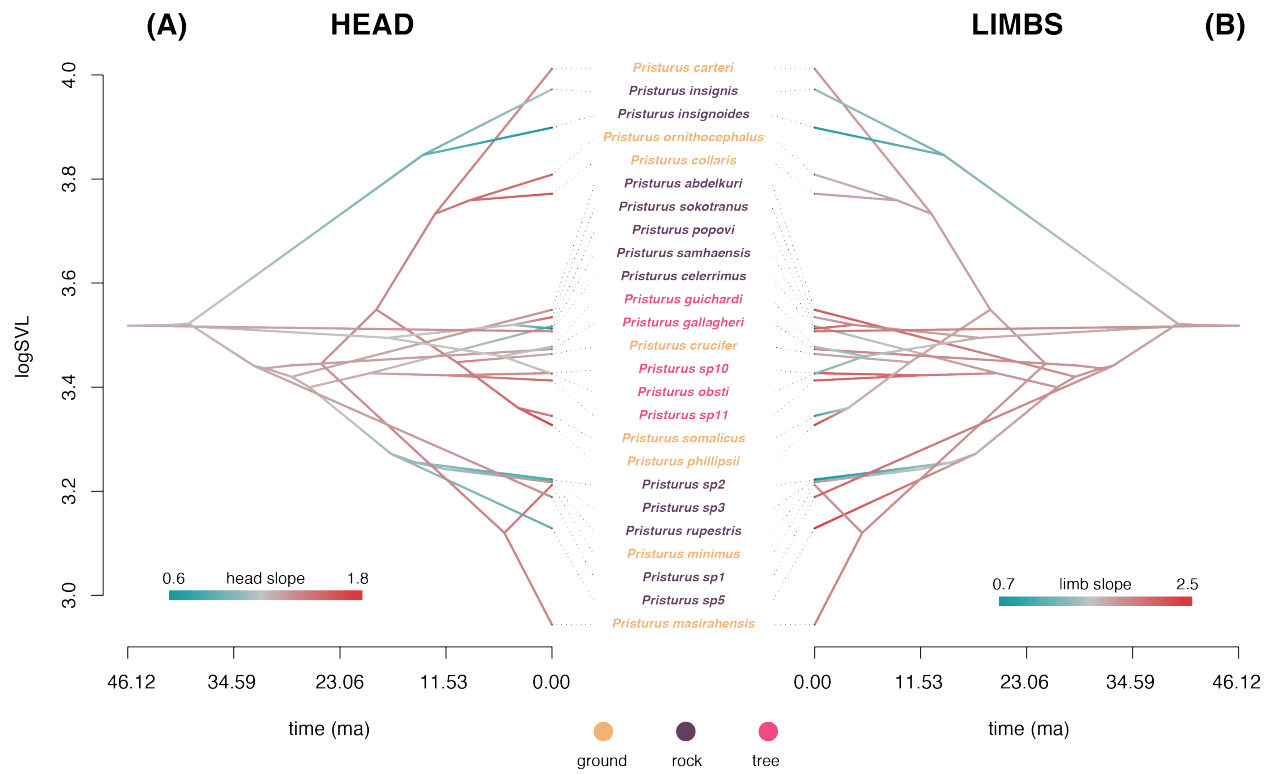


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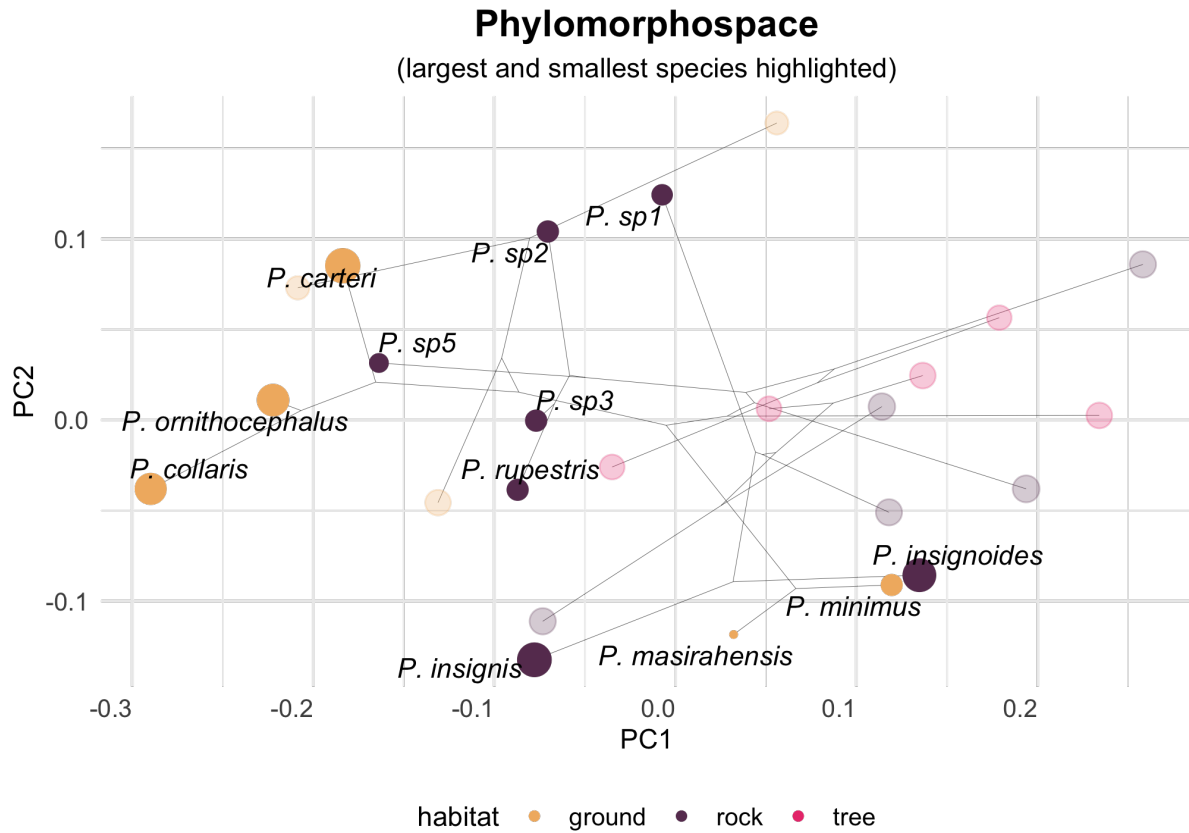


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