Evolution along allometric lines of least resistance: Morphological differentiation in *Pristurus* geckos

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Abstract

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Introduction

Understanding how phenotypic diversity evolves, and elucidating the forces that generate and maintain this diversity, are major goals in evolutionary biology. Because adaptive evolution is the product of natural selection, changes in ecological selection pressures are expected to affect the evolutionary trajectory of phenotypic traits that facilitate an organism's survival in their habitat. Evolutionary theory predicts that differing habitats will exert unique ecological selection pressures on organisms, resulting in associations between ecological and phenotypic traits. Indeed, species inhabiting differing habitats often display functional, behavioral, or phenotypic differences, that have presumably been the result of adaptive diversification in their respective ecological habitats (Collar et al. 2010; Kaliontzopoulou et al. 2015; Price et al. 2015; Martinez et al. 2021; Kolmann et al. 2022).

One possible evolutionary outcome of ecological specialization is that organisms inhabiting similar environments display common phenotypic characteristics. When such patterns occur repeatedly (e.g., Losos 1992; Schluter and McPhail 1992), this convergent evolution is treated as strong evidence of adaptation. Indeed the ecomorphological paradigm (sensu Arnold 1983) is predicated, in part, on such cases, which emphasize the strong association between the phenotypic traits that organisms display (morphological, behavioral, or physiological), and the ecological characteristics of their habitat that mediate organismal performance. In vertebrates, ecomorphological trends have been well studied in numerous taxonomic groups, and include the emblematic 'ecomorphs' of Caribbean *Anolis* lizards that exploit different microhabitats (Losos 1992, 2009; Mahler et al. 2013), differential beak morphology in species of Darwin's finches (Schluter and Grant 1984; Grant and Grant 2006; Reaney et al. 2020), the recurring phenotypes of African lake cichlids across ecological regimes (Albertson and Kocher 2001; Urban et al. 2022), and the distinct body forms of freshwater fishes in benthic and limnetic habitats (Jastrebski and Robinson 2004; Berner et al. 2008; Stuart et al. 2017) among others.

However, while the patterns of morphological differences in distinct ecological contexts have been well documented, less-well understood is how this differentiation has been influenced by the covariance between body parts resulting from body size variation (i.e., allometry). It has long been recognized that the interrelationships among traits can have a strong influence on how phenotypic evolution proceeds, as trait correlations influence the degree to which phenotypic variation is exposed to selection (Wagner and Altenberg 1996). Thus, the integration among traits can constrain phenotypic change in certain directions, or enhance variation along other phenotypic axes (Schluter 1996; Wagner and Altenberg 1996; Wagner and Zhang 2011; Klingenberg and Marugán-Lobón 2013; Goswami et al. 2014, 2016; Felice et al. 2018; Navalón et al. 2020). Further, because nearly all linear traits covary strongly with overall body size (Jolicoeur 1963; Bookstein 2022), allometric trends could be considered the quintessential expression of phenotypic integration. Thus, identifying whether allometric patterns differ across habitats, and how such patterns of trait covariation affect ecomorphological trends among species utilizing those habitats, remains an important question worthy of investigation.

The Afro-Arabian geckos in the genus *Pristurus* afford the opportunity to elucidate the interdigitating effects of allometry and habitat specialization on clade-level patterns of phenotypic diversity. Prior work on this system (Tejero-Cicuéndez et al. 2021a) revealed that the colonization of ground habitats has been a trigger of morphological change, specifically reflected in an increase in body size and shape disparity. Interestingly, some ground-dwelling species are among the largest of the genus and also show increased relative head sizes and limb proportions, while some other species with this ecological specialization have evolved to be among the smallest of the group. Additionally, among the species exploiting rocky habitats (the most common ecological feature in *Pristurus*), there are also species with both considerably large and small body sizes (Tejero-Cicuéndez et al. 2021a). What remains unexplored, however, is how the evolution of body shape is related to differences in body size and whether habitat specialization has an impact in this shape-size relationship.

In this study, we employed a combination of multivariate morphometric and phylogenetic comparative analyses to interrogate macroevolutionary patterns of evolutionary allometry in *Pristurus* geckos of Afro-Arabia. Using phenotypic, phylogenetic, and ecological data, we first characterized allometric trends in body form in the group, to discern the extent to which evolutionary allometric trends across the phylogeny aligned with habitat-based static allometry for species occupying distinct ecological regimes. We then examined changes in allometric trends across the phylogeny, and linked these patterns to overall phenotypic integration, diversification in morphospace, and habitat utilization among taxa. Our analyses revealed that patterns of evolutionary allometry across species aligned with allometric trends within habitats, demonstrating that the interplay between ecological specialization and allometric trajectories in species with disparate body size may have played a determinant role in shaping the phenotypic evolution and hence in adaptive dynamics in this clade.

Materials and Methods

Data

We used a combination of phenotypic, phylogenetic, and ecological data to characterize and evaluate intra- and interspecific allometric trends. The data utilized here were obtained from our prior work on this system (Tejero-Cicuéndez et al. 2021a, 2022), and are briefly described here. First we used a time-dated, molecular phylogeny that included all members of the genus *Pristurus*, including several currently undescribed taxa. The tree was estimated in a Bayesian framework, using five mitochondrial markers, six nuclear markers, and 21 calibration points (for details see Tejero-Cicuéndez et al. 2022). Next we categorized each species as belonging to one of three ecological groups (ground, rock, or tree), based on descriptions of habitat use found in the literature (see Tejero-Cicuéndez et al. 2021a). Finally, we obtained a phenotypic data set containing 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 nine or more individuals; resulting in a dataset of 687 individuals from 25 species (invidivuals 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.xwdbrv1f6 (Tejero-Cicuéndez et al. 2021b).

Statistical and Comparative Analyses

We conducted a series of analyses to interrogate allometric trends, patterns of integration, and macroevolutionary changes in allometry, relative to differentiation in body form. First we characterized evolutionary allometry in the genus by performing a phylogenetic multivariate regression of body form on body size (i.e., SVL), using the species means as data. We then performed an analogous procedure at the individual level, regressing body form on body size using our entire dataset. From both the species-level (phylogenetic) and the individual-level analyses, we obtained the set of regression coefficients, and calculated the difference in their angular direction to describe the extent to which patterns of allometry at the individual level were concordant with evolutionary allometric trends across species.

Next we used the dataset containing all individuals to determine whether trends in static allometry differed across habitat groups. This was accomplished by performing 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). We then 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). Patterns of multivariate allometry relative to body size were visualized 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.

Additionally, because allometry describes the extent to which traits covary with body size and with each other (i.e., integration), we conducted an analysis of integration. Here we characterized the extent of morphological integration in body form for individuals within each habitat group. Integration was estimated by summarizing the dispersion of eigenvalues of the trait covariance matrix (sensu Pavlicev et al. 2009). This measure (V_{rel}) was subsequently converted to an effect size (a Z-score), which quantified the strength of morphological integration (Conaway and Adams 2022). We then performed a series of two-sample tests to compare the strength of morphological integration across habitat groups, following the procedures of Conaway and Adams (2022). Additionally and for comparison, we repeated these analyses on the set of size-standardized trait data, found as a set of shape ratios (sensu Mosimann 1970) where each trait was divided by body size (Supplemental Information).

To determine the extent to which static and evolutionary allometry were concordant, we evaluated the directions in morphospace of both the evolutionary (species-level) and static (habitat-based) allometric trends. Specifically, we we obtained the set of regression coefficients from both the phylogenetic multivariate regression and the multivariate analysis of covariance analyses above, and calculated the differences in angular direction between the evolutionary trajectory and the static allometry trend for each habitat group. The observed angles were then statistically evaluated relative to empirical sampling distributions obtained through permutation (RRPP), based on a null model containing habitat groups but lacking an allometric component.

Next, to discern how allometric trends resulted in the evolution of distinct body forms, we examined changes in the body shape proportions across the phylogeny. Here we treated the head dimensions and limb dimensions separately, as allometric trends could potentially differ between these body regions due to differential functional or selective constraints (Kaliontzopoulou et al. 2010). Because both the head and limb data were multivariate, we first performed a partial least squares (PLS) analysis (Rohlf and Corti 2000) of the head traits versus SVL, and the limb traits versus SVL, to describe the direction of maximal covaration between each body region and size. Then, we measured the mean residuals of each species to the allometric trend inferred, which show if head and limbs proportions of species are greater or smaller than expected for their body size. The species residuals were then mapped on the phylogeny of *Pristurus* using a

Brownian motion model of evolution, to qualitatively evaluate shifts in head and limbs proportionality across the phylogeny for the group. Similarly, within-species patterns of static allometry were visualized by plotting regressions of PLS scores on SVL for both head and limb traits separately.

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. Additionally, representative specimens (scaled to unit size) were also visually compared to aid in describing these trends. A similar phylomorphospace was constructed for species means not corrected for body size, and the phenotypic disparity among species means in each habitat was calculated and subsequently compared (Supplemental Information). 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 `geomorph` 4.0.4 (Baken et al. 2021), and scripts written by the authors (available at **XXX**).

Results

Using phylogenetic regression, we found significant evolutionary allometry in body form across species ($N_{sp} = 25$; $F = 217.9$; $Z = 5.53$; $P < 0.001$). Likewise, when allometry in body form was examined across individuals, a similar pattern was observed ($N_{ind} = 687$; $F = 7910.8$; $Z = 9.20$; $P < 0.001$). Further, the vectors of regression coefficients between the two analyses were highly correlated ($\rho = 0.94$) and were oriented in nearly parallel directions in morphospace ($\theta = 1.49°$). This revealed that the pattern of multivariate allometry across individuals was concordant with macroevolutionary trends of interspecific allometry among species of *Pristurus* across the phylogeny.

Our analyses also exposed significant differences in the allometry of body form among *Pristurus* utilizing distinct habitats (Table 1). Here, 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). In addition, allometric patterns in both rock and tree habitats were similar to the multivariate line of isometry (Figure 2), while patterns of multivariate allometry in ground-dwelling *Pristurus* was decidely steeper. Inspection of the regression coefficients for each trait (Supplemental Information) confirmed the steeper allometric coefficients for all head and limb traits in ground-dwelling *Pristurus* as compared with rock and tree-dwelling taxa, corroborating this result. Taken together, these findings implied that larger individuals of ground-dwelling *Pristurus* species displayed disproportionately larger heads and limbs, as compared with large individuals in taxa utilizing other habitat types. Multivariate visualizations of these multivariate allometric trends (Figure 2) confirmed these statistical findings, and indicated that the allometric trajectory in ground-dwelling *Pristurus* was more extreme as compared with either rock or tree-dwelling *Pristurus*.

Examination of patterns of trait covariation revealed strong levels of morphological integration within each habitat type ($Z_{ground} = 3.97$; $Z_{rock} = 3.72$; $Z_{tree} = 2.15$). Further, two-sample tests revealed that the strength of morphological integration was significantly greater in ground-dwelling *Pristurus* than either those utilizing rock ($Z_{Groung-Rock} = 6.59$; $P << 0.001$) or tree habitats ($Z_{Groung-Tree} = 11.17$; $P << 0.001$). *Pristurus* utilizing tree habitats displayed the lowest levels of integration, which were also significantly less than in the rock habitat ($Z_{Rock-Tree} = 7.19$; $P << 0.001$). When size was accounted for in the data, levels of integration dropped considerably, though the overall pattern and differences among habitat groups remained the same (Supplemental Information).

Comparisons of evolutionary allometry with static allometry in each habitat revealed substantial concordance between allometric trends at both the species and population levels. Here, the vectors of regression coefficients representing evolutionary allometry and those representing static allometry within habitat groups were oriented in nearly parallel directions in morphospace, with small pairwise angles between them ($\theta : 2.5° \rightarrow 6°$). Subsequent permutation tests indicated that they were significantly more congruent than expected (Table 3). Thus, in *Pristurus*, static and evolutionary allometry trends were essentially parallel, indicating a direct correspondence between the two. This result implied that phenotypic evolution across species aligned closely with directions of allometric variation within habitat groups at the individual level.

Mapping the residuals of species into the phylogeny showed that large ground-dwelling species displayed greater head proportions than large rock-dwelling species, who exhibited smaller heads relative to body size (Figure 3A). Conversely, the opposite pattern was observed when comparing small species utilizing these habitats: ground-dwelling species showed small relative head proportions while rock-dwelling species displayed generally larger head proportions. In contrast, limb shape showed more variable patterns. Although all large ground-dwelling species consistently displayed large relative limb proportions, large rock-dwelling species were more variable in this trait, with *P. insignis* exhibiting large and *P. insignoides* small limb proportions. For small species, shifts in relative limb proportions seemed more independent of habitat utilization, since there were differences in limb residuals both within rock- and ground-dwelling species (Figure 3B). Visual inspection of static allometry trends within species (Figure 4) largely confirmed these patterns, illustrating that large ground-dwelling species displayed steeper allometry as compared with large rock-dwelling species. Overall there was general concordance across taxa in terms of trends of multivariate allometry, affirming that the association between evolutionary allometry and habitat-based static allometry was robust.

Viewing body shape differentiation in *Pristurus* in phylomorphospace (Figure 5) revealed broad overlap among habitat groups, though arboreal (tree-dwelling) species were somewhat more separated in morphospace. Rock-dwelling species occupied a slightly larger region of morphospace as compared with the other groups, though this pattern was not statistically significant (Supplemental Information). Intriguingly, when viewed in relation to body size, large *Pristurus* species were not localized to a particular region of morphospace, nor were smaller species. Instead, the largest rock-dwelling species were found in close proximity to the smallest ground-dwelling species, indicating that they were similar in overall body shape. Likewise, the smaller rock-dwelling species were found close to large ground-dwelling species in morphospace, indicating they displayed similar body shapes as well.

Finally, when representative specimens were scaled to a similar body size (Figure 6), the consequences of differences in allometric trends on body proportions became apparent. Here, larger ground-dwelling *Pristurus* species displayed disproportionately larger heads and limbs as compared with large *Pristurus* species utilizing other habitat types. Conversely, smaller rock-dwelling *Pristurus* species were found to have disproportionately larger heads and limbs as compared with smaller *Pristurus* ground-dwelling species. These patterns confirmed those identified in morphospace (Figure 5), where large ground-species were similar in body form to small rock-dwelling species, while small ground-dwelling species were similar in body form to large rock-dwelling species (Figure 6). Thus, synthesizing the patterns revealed in the phylomorphospace with those identified in our earlier analyses revealed a complex interplay between body shape, body size, habitat use, morphological integration, and multivariate allometry; where species with similar body shapes displayed differing overall size, were found in distinct habitats, and exhibited different allometric trends.

Discussion

The relationship between certain phenotypic traits and the organisms' environment is a central paradigm in evolutionary biology. In this context, disentangling the causes of phenotypic differentiation is essential to understand how natural selection operates. In this study, we evaluated the role of potential drivers of body shape differentiation in the geckos of the genus *Pristurus*. To this end, we investigated the interplay of ecological specialization, phenotypic integration and allometric trends to decipher how they have shaped patterns of morphological evolution in this radiation of Afro-Arabian geckos. Our results show that allometric trends and integration patterns are different across habitats, with ground-dwelling species having the steepest multivariate allometric slope and also the strongest morphological integration. These patterns are also different across body parts, with decoupled trends between head and limb proportions. Additionally, we found that changes in static allometric trends are not restricted to specific regions of the phylogeny, but rather they show multiple independent increases and decreases following common dynamics within habitat groups. Overall, these results suggest that the interplay between allometric and integration patterns is a fundamental factor to explain the morphological evolution across a variety of habitats, which is consistent with the theoretical expectation that different ecological contexts impose distinct selective pressures triggering phenotypic change.

REDO A BIT. Emphasize commonalities first, then differences.

- result 1: allometry; overall trend among species nearly identical to that among individuals.

Patterns of multivariate allometry in body form calculated from individuals were found to be nearly identical to those calculated from per-species means in Pristurus geckos. Specifically, the vectors of regression coefficients of the two analyses are virtually parallel ($\theta = 1.49°$), indicating that the evolutionary allometry is not substantially different whether measured with individual measurements or with species means in this genus.

??We also explored patterns of static allometry to compare them among species and with general trends of evolutionary allometry.

- result 2: Allometry differs among habitat groups: 'steeper' allometry in Ground-dwelling (implication: disproportionately larger heads and longer limbs in species at larger body sizes).

When we compared multivariate allometric slopes of species occupying different habitats, we found that, while rock-dwelling and arboreal species do not significantly differ from the isometric trend, ground-dwelling species have a steeper slope which is statistically different from isometry. This means that large ground-dwelling *Pristurus* present disproportionately larger heads and longer limbs relative to other large species, while small species in the ground have disproportionately smaller heads and shorter limbs (**Figure residuals traitgrams**). This is consistent with previous results on the morphological evolution of *Pristurus* (Tejero-Cicuéndez et al. 2021), where large ground species were indeed found to have also disproportionately large heads and long limbs. This suggests that the segregation in body size and shape through differential allometric relationships across habitats responds to adaptive dynamics concerning the colonization of ground habitats, and perhaps with a particular interest of hard ground environments inhabited by the largest ground-dwelling species (including the largest of the genus, *P. carteri*), which has already been suggested to be the main driver of the morphological evolution in this genus (Tejero-Cicuéndez et al. 2021). This points toward the existence of a specialized form of *Pristurus* geckos adapted to hard grounds (e.g., **some**

definition of hard ground vs. soft grounds??), illustrating the ecomorphological relationships in the genus with a rather conspicuous 'ecomorph' (see Figure X for an example of the hard-ground ecomorph, *P. carteri*).

- result 3: relationship between evolutionary and static allometry, evolution of static allometry mapped in the phylogeny…

There is no general consensus about the relationship between the three types of allometry: ontogenetic (allometry during the development), static (allometry among individuals at the same developmental stage), and evolutionary (allometry across populations or species). This, in turn, is reflected in the broadly ambiguous interpretation of allometric patterns in the literature, with an often uncertain distinction between allometry as an evolutionary constraint and allometry as functional optimization resulting from natural selection (Pélabon et al. 2014, Voje et al. 2014). Even though testing these alternative hypotheses is beyond the scope of this work, our results do suggest that static and evolutionary allometry are very similar in *Pristurus* geckos, which could be explained by low evolvability of allometry, but also by the effect of relatively homogeneous selective pressures at different scales. Further analyses, for instance including a broader phylogenetic context and developmental assessments, are needed to illuminate the relationships between different levels of allometric trends. **EXTEND THIS**

- result 4: Morphological integration differs among habitat groups. Strongest in ground-dwelling; weakest in tree-dwelling. SOME MEANING (combined with allometric trend implies that patterns of trait covariation are more constrained within ground-dwelling…. Thus, differences in body form are most likely found along this primary axis… (harken to Schluter evolution along lines of least resistance)
  - Additionally, rank-order of magnitude of integration across habitat groups corresponds with the range of body sizes in each: ground-dwelling display the largest size-range, while tree-dwelling the least (Supp. Information). On the one hand this matches the expectation that much of the integration observed in *Pristurus* is the result of allometric trends…. And the fact that levels of integration drop so precipitously when data are size-standardized are in accord with this interpretation. Nevertheless, when size is accounted for, the rank-order of magnitudes of integration remain the same,

implying that ground-dwelling *Pristurus* are still relatively constrained in patterns of trait covariation as compared with the other two groups.

  - This notion was further supported when viewing the phylomorphospace of the species means not adjusted for size (SI). Here (and not surprisingly), PC1 is dominated by size, with small species at one end and larger species at the other. More importantly however, is that the disparity among species utilizing different habitats differed significantly in this space. Here, ground-dwelling displayed significantly greater phenotypic disparity than did the other groups (SI).

Similarly, when analyzing patterns of morphological integration, we found important differences among habitat groups: ground-dwelling species present the strongest integration, which in turn is weakest in arboreal species. Morphological integration occurs when different body parts coevolve, and has been suggested as an evolutionary constraint, since it restricts the specific lines along which integrated structures are allowed to vary (**REF**). Weaker integration levels (i.e., modularity), on the contrary, might facilitate morphological evolution by allowing a less constrained exploration of the morphospace (**REF**). However, integration might also be interpreted as a potential driver of morphological change, since it may provide a phenotypic pathway through adaptive lines of least resistance that enable rapid evolutionary processes (Navalón et al. 2020). In this context, our results on allometry and integration suggest that patterns of trait covariation are more constrained in ground-dwelling species, such that their differences in body form are most likely found along this primary axis. The fact that ground species in *Pristurus* have been found to have the widest phenotypic disparity and highest rates of morphological evolution (Tejero-Cicuéndez et al. 2021) is consistent with the idea that integration patterns are acting to facilitate morphological evolution along lines of least resistance.

- result 5: morphospace: Thus there was a reciprocal relationship between body shape and body size across ground-dwelling and rock-dwelling species. SOMEHOW TIE THIS TO integration (DCA pondering this one)
- one interesting… head vs. (correlation of head vs. limb slopes: 0.42. Pretty low. Implies some sort of differential something here, resulting in distinct allometric patterns for these

two body regions. SImilar to Antigoni's work (and refs therein). IMPLICATION: tie this into integration/modularity. Less integrated across the whole organism, and more modular… Future studies should examine this.

Another insightful result is the low correlation between head and limbs in their allometric slopes, which implies different evolutionary trajectories for these two body regions. This is likely to happen when different parts of an organism are subjected to different functional pressures (e.g., head evolution might be mainly influenced by diet while limb evolution might respond more tightly to the substrate used by the species), resulting in a decoupling of their respective morphological change. Ultimately, the combination of selective pressures upon which organisms evolve may lead to differential levels of integration across different body parts, with certain structures coevolving in a similar (i.e., integrated) manner and others in a segregated (i.e., modular) way. This, in turn, may have fundamental implications for the extent of morphological diversification within clades, and can be key to describe the phenotypic divergence observed across the tree of life. Future and more in-depth studies on the evolution of different body parts in *Pristurus* and other lizards, including for instance finer phenotypic data and comprehensive ecological information, may allow for discerning the functional drivers of head and limb evolution.

- In conclusion… -Synthesizing these patterns together … (summarize: steeper allometry, higher integration, greater disparity in body size and body form all in ground-dwelling species). TOgether the patterns uncovered in our study imply that phenotypic diversification among ground-dwelling *Pristurus* follows tightly along its allometric trajectory, as evidenced by the higher disparity and stronger morphological integration…. some reference back to Goswami 'fly in a tube' paper. Thus, *Pristurus body forms appear to diversify along* allometric* lines of least resistance…. (Schluter ref again)

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

	Df	SS	MS	Rsq	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 static allometry across habitats. 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

Table 3: Pairwise comparisons of multivariate evolutionary allometry versus static allometry for each habitat group. Pairwise angular differences between evolutionary and static allometry ($\theta_{E,S}$), their associated effect sizes ($Z_{\theta_{E,S}}$), and significance levels are displayed. Significance levels evaluate whether the observed angle is smaller than expected (i.e., vector directions are similar).

	$\theta_{E,S}$	$Z_{\theta_{E,S}}$	P-value
Ground	2.371	-1.856	0.001
Rock	4.553	-1.638	0.006
Tree	5.955	-1.556	0.027

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).

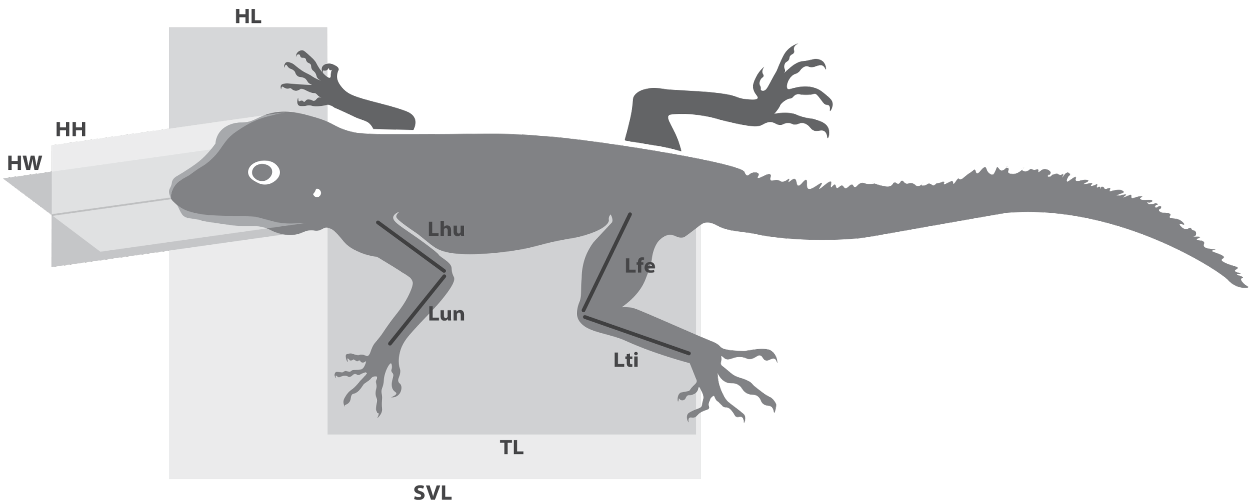
Figure 2. Plot of regression scores and predicted lines representing the relationship between linear body measurements and size (SVL). Individuals are colored by habitat use: ground (beige), rock (dark purple), and tree (magenta). Isometric trend represented by the dashed line.

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 residuals from phylogenetic regressions 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: ground (beige), rock (dark purple), and tree (magenta).

Figure 4. Patterns of static allometry for each species for head traits (upper panel) and limb traits (lower panel). Species are separated by their habitat groups and colored by the magnitude of their regression slope (red: steeper slopes, blue: shallower slopes).

Figure 5. Phylomorphospace of *Pristurus*, based on residuals from a phylogenetic regression of body measurements on size (SVL). Species means are colored by habitat use: ground (beige), rock (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.

Figure 6. Representative specimens from large and small *Pristurus* species, colored by habitat use: ground (beige) and rock (dark purple). Specimens are scaled to a common body size (SVL) to emphasize the relative differences in limb and head proportions. Original scale shown as the gray bar.



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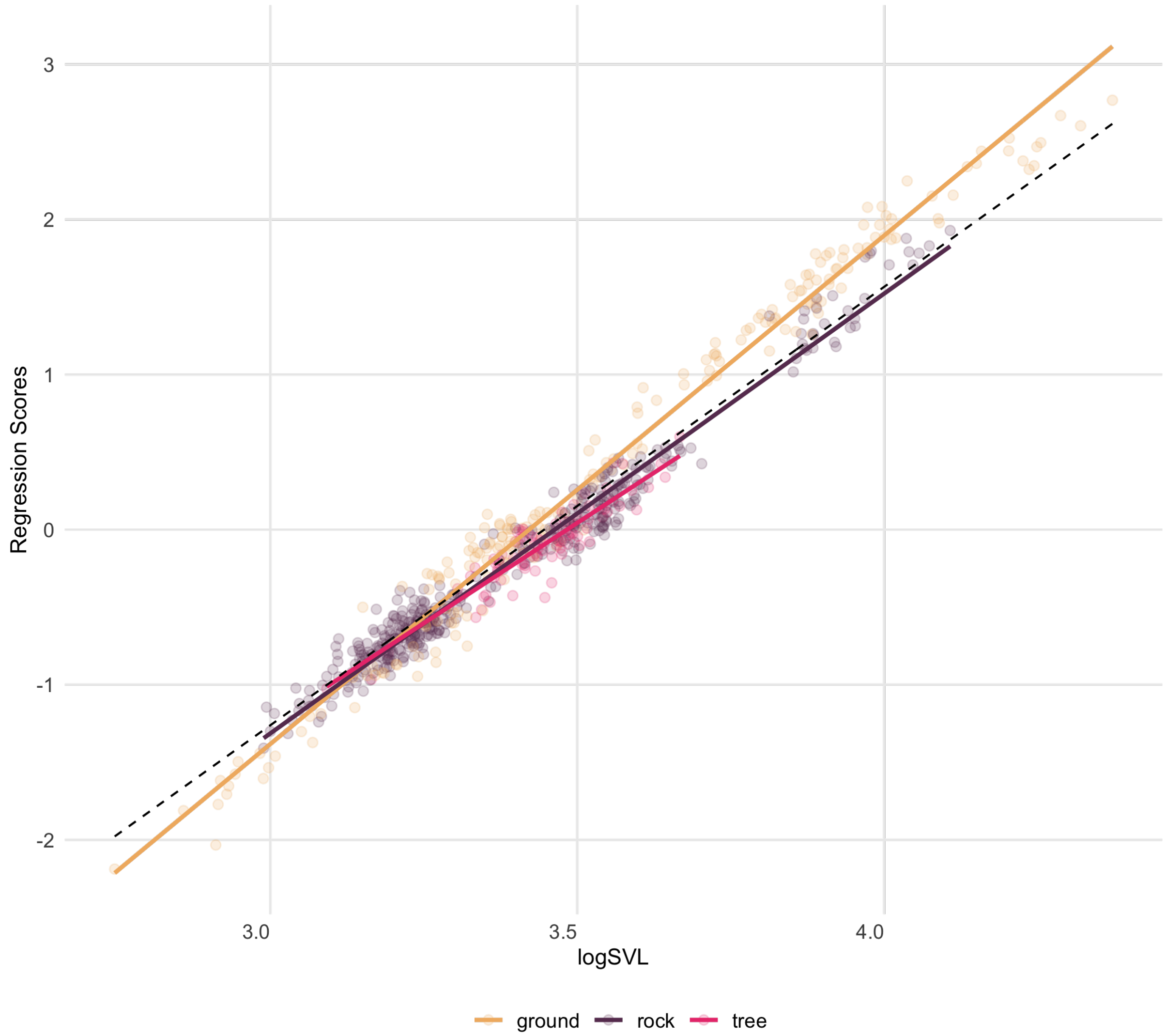

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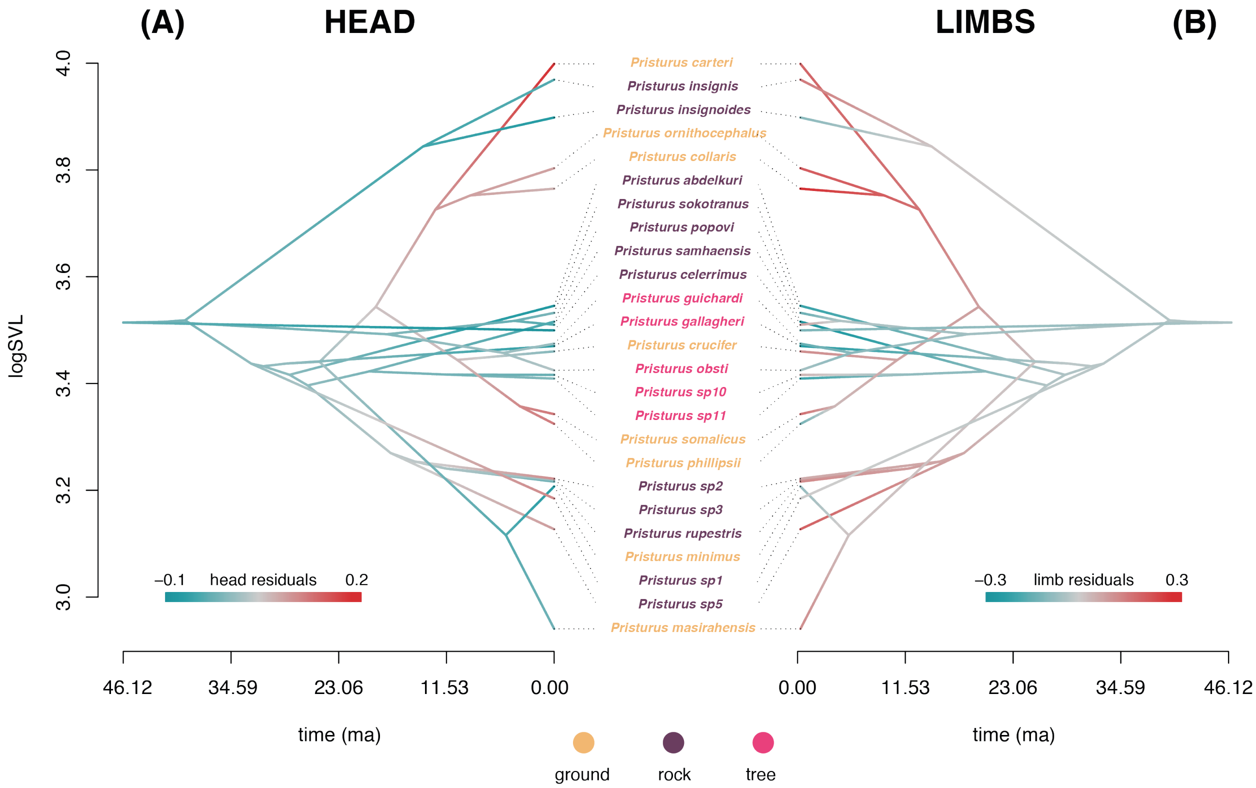

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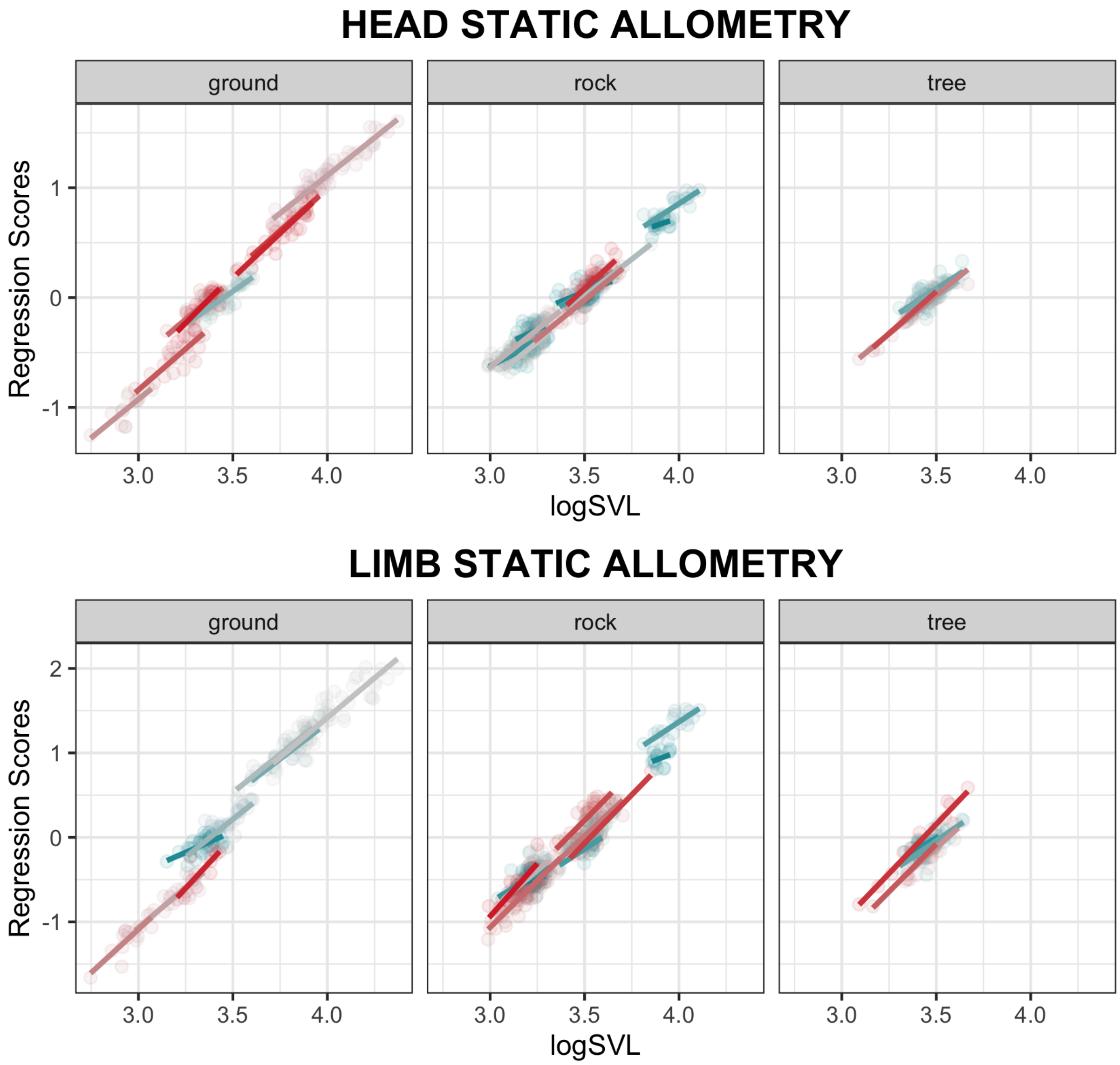

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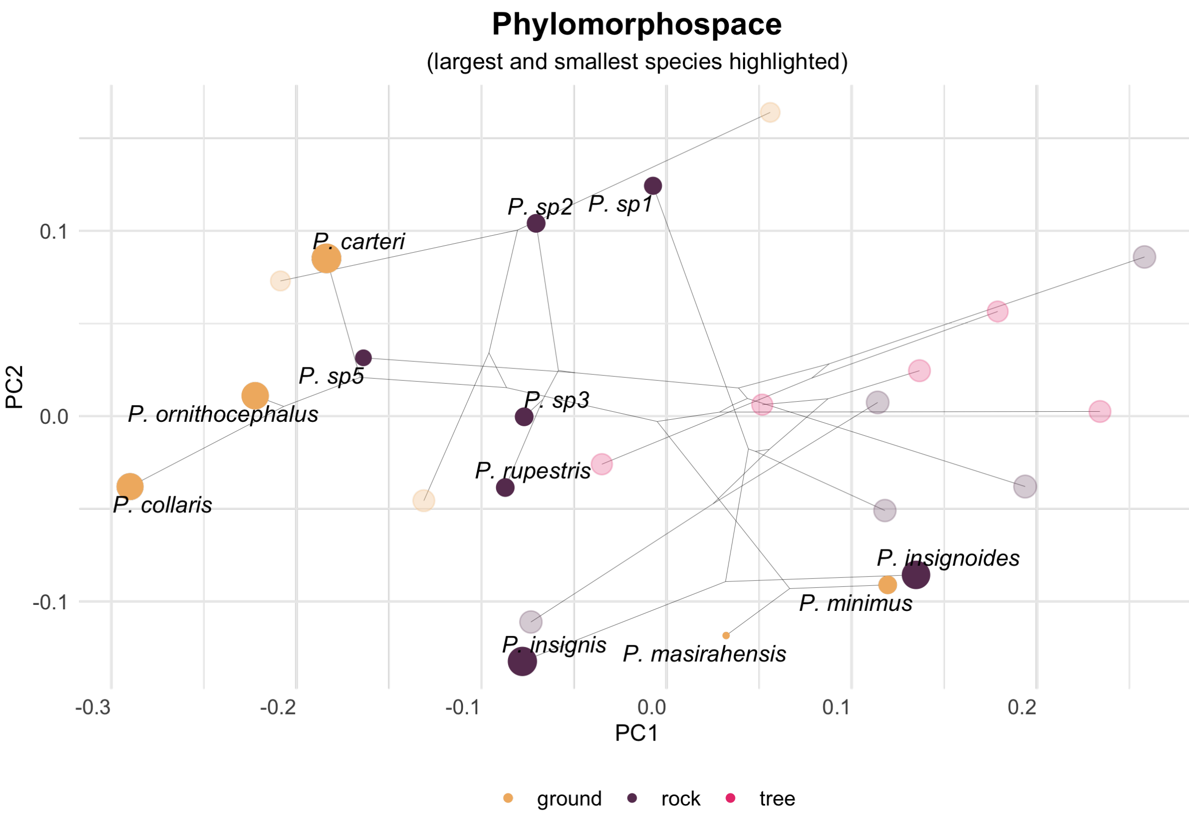

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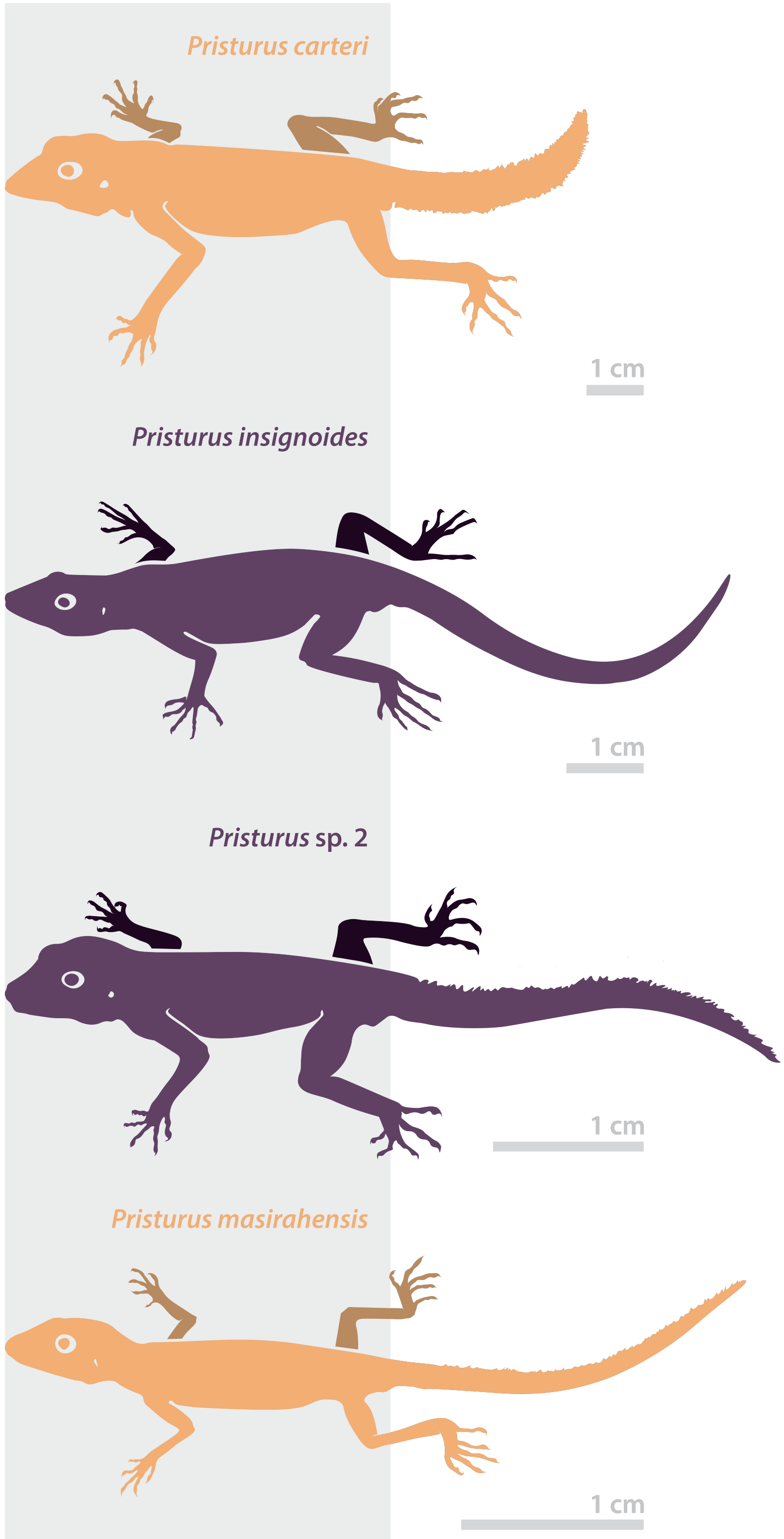

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