The role of habitat and evolutionary allometry in the morphological differentiation of *Pristurus* geckos

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Short Title: XXX

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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~~ 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 benthis 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). Further, because nearly all linear traits covary strongly with overall body size (Jolicoeur 1963; Bookstein 2022), allometric trends could be considered the quintessential measure 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 understudied question worthy of investigation.

The Afro-Arabian geckos in the genus *Pristurus* afford the opportunity to elucidate the inter-digitating 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 ~~relationship~~ shape-size ~~. (how the size-shape relationshipdiffers among habitats.)~~ relationship.

In this study, we employed a combination of multivariate morphometric and phylogenetic comparative analysis 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 allometric patterns differed across species occupying distinct ecological habitats. We then examined changes in allometric trends across the phylogeny, and linked these patterns to overall phenotypic diversification in morphospace, and in relation to habitat utilization. Overall our results demonstrate that the interplay between ecological specialization and differing allometric trajectories ~~across habitats can result in similar overall phenotypes, even when those species display differing body sizes across habitat types~~ ~~**maybe some other general ending sentence here?**~~in species with disparate body size may have a determinant role in shaping the phenotypic evolution and hence in adaptive dynamics at the clade level.

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 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 size, using the species means as data. We then performed an analogous procedure at the individual level, regressing body form on size using our entire dataset. From both the species-level (phylogenetic) and the individual-level regression models, we obtained the set of regression coefficients, and calculated the difference between them 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 individual dataset to determine whether allometric trends in body form 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.

We then examined changes in allometric trends 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 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. PLS scores from each analysis were obtained, and species-specific slopes describing the extent of head and limb allometry within each species were extracted from an analysis of covariance modeled as: $PLS1_{head} \sim SVL * species$ and $PLS1_{limb} \sim SVL * species$ respectively. The species-specific allometric slopes were then mapped on the phylogeny of *Pristurus* using a Brownian motion model of evolution, to qualitatively evaluate shifts in allometry across the phylogeny for the group (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

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 ~~multivaraite~~ 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 proportionately larger heads and limbs, as compared with large individuals in taxa utilizing other habitat types. A visualization of multivariate allometric trends (Figure 2) confirmed these statistical findings, and indicated that the allometric trajectory in ~~rock-dwelling~~ ground-dwelling animals was more extreme as compared with either ~~ground~~ rock or tree-dwelling *Pristurus*.

When allometric patterns were mapped on the phylogeny, traitgrams elucidated that changes in allometric trends were not concentrated to specific regions of the phylogeny (Figure 3). Rather, increases and decreases in allometry of both the head traits and the limb traits occurred repeatedly (see also Supplemental Information). When these patterns were viewed relative to body size, large ground-dwelling species tended to display steeper head allometry as compared to large rock-dwelling species~~;~~, who displayed shallower head allometry (Figure 3A). Likewise, a similar pattern was observed when comparing small species utilizing these habitats. In contrast, large ground-dwelling species exhibited intermediate patterns of limb allometry, and small species in general were more variable in ~~their patterns of limb allometry~~ such patterns (Figure 3B). Inspection of traitgrams thus revealed some degree of discordance in patterns of allometry across body regions; a pattern evidenced by the relatively low correlation between slopes representing head and limb allometry respectively ($\rho = 0.42$).

When body shape differentiation in *Pristurus* was viewed in phylomorphospace (Figure 4), we found 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, integrating the patterns revealed in the phylomorphospace with those identified in our earlier analyses revealed a complex interplay between body shape, body size, habitat use, and multivariate allometry; where species with similar body shapes displayed differing overall size, were found in distinct habitats, and exhibited different allometric trends.

Discussion

- First paragraph; restate topic/questions (see last par of Intro); summarize general findings ...
    - something about linking allometry and phenotypic diversification?
- result 1: implication
- result 2: implication
- result 3: implication
    - morphospace: Thus there was a reciprocal relationship between body shape and body size across ground-dwelling and rock-dwelling species.
- 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.

closing paragraph

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

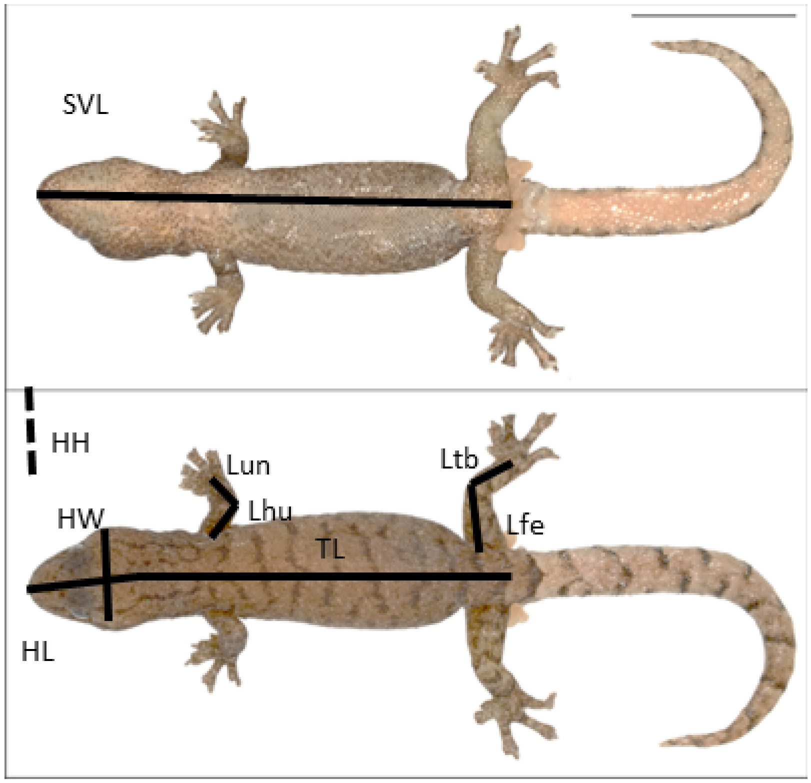
Figures

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 ~~re~~ are colored by habitat use: ~~rock~~ ground (beige), ~~ground~~ 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 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~~ ground (beige), ~~ground~~ rock (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~~ grou d (beige), ~~ground~~ 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.



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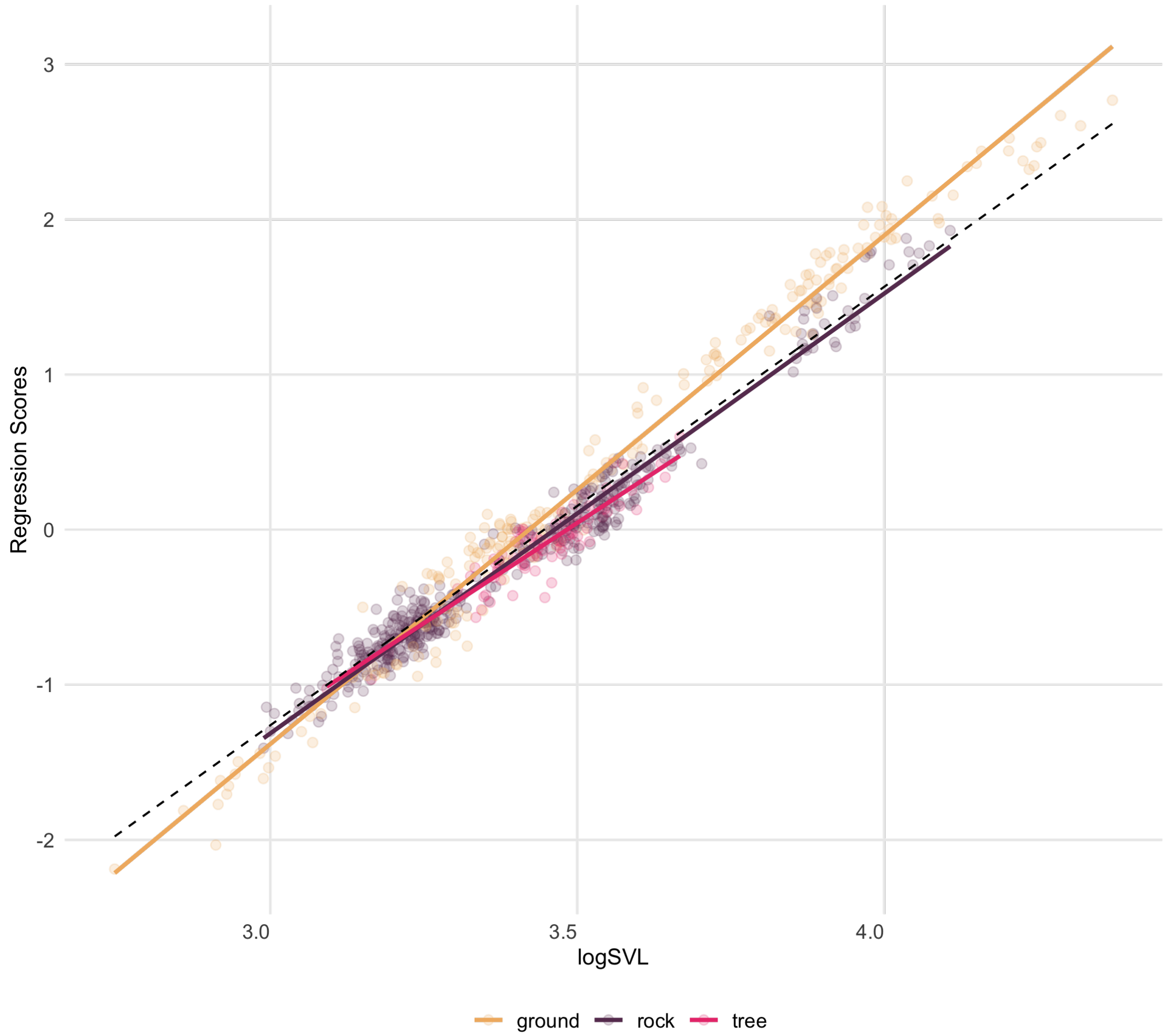

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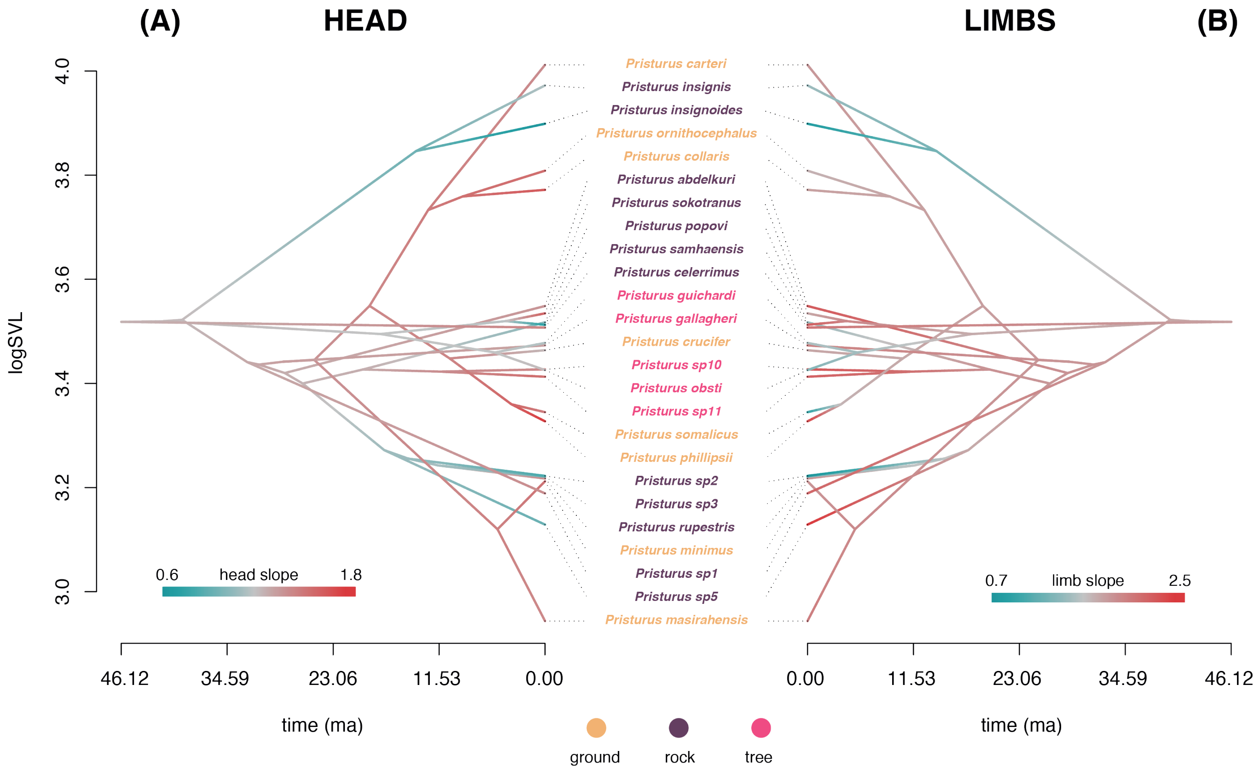

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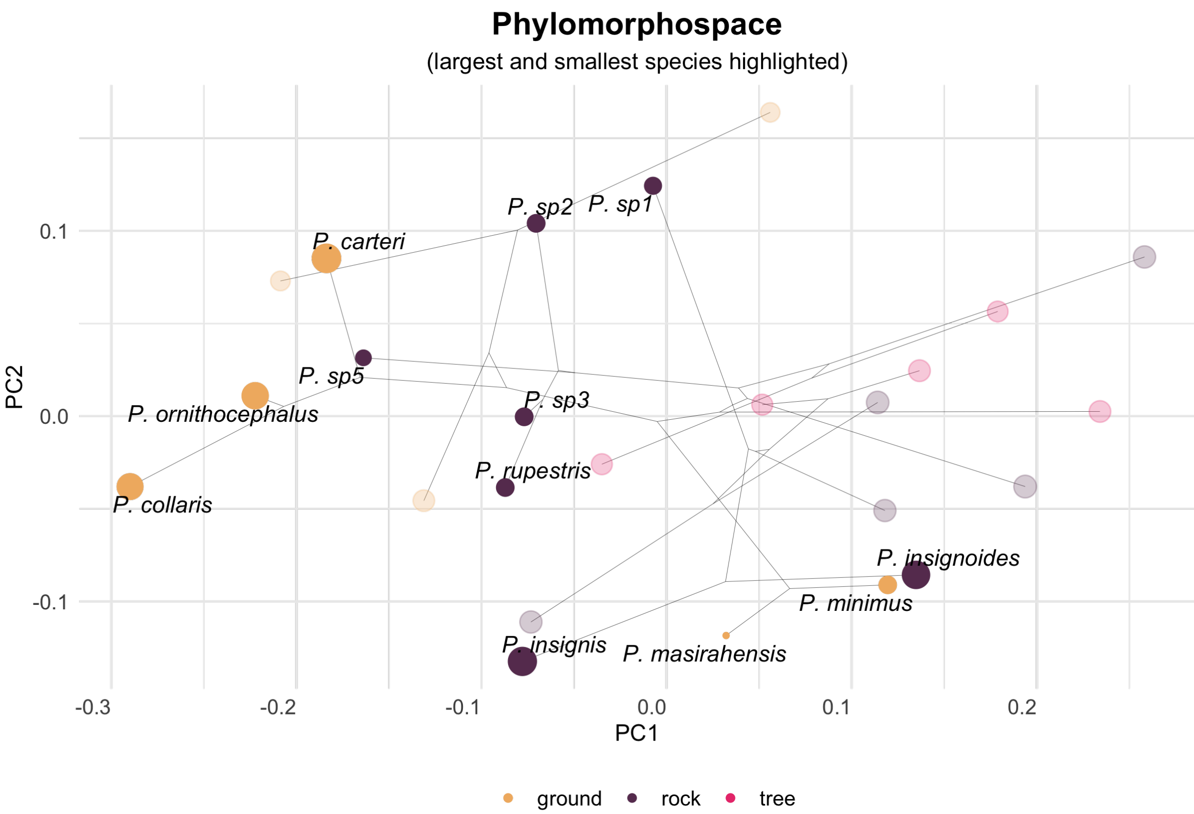

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