

1 **Leaf shape modulates climate–trait relationships in the wild species**

2 ***Chenopodium hircinum* (Amaranthaceae)**

3 Jonatan Rodríguez¹, Vilma Quipildor¹, Eugenia Giamminola^{1,2}, Sergio J. Bramardi³,

4 David Jarvis⁴, Jeff Maughan⁴, Jiemeng Xu⁵, Hafiz U. Farooq⁵, Pablo Ortega-Baes^{1,2},

5 Eric Jellen⁴, Mark Tester⁵, Daniel Bertero⁶ and Ramiro N. Curti^{1,2*}

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7 ¹Laboratorio de Investigaciones Botánicas (LABIBO), Facultad de Ciencias Naturales,

8 Universidad Nacional de Salta, Av. Bolivia 5150, Salta, Argentina.

9 ²Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) CCT Salta-

10 Jujuy, Argentina.

11 ³Centro de Investigaciones en Toxicología Ambiental y Agrobiotecnología del

12 Comahue (CITAAC-CONICET), Universidad Nacional del Comahue, Neuquén,

13 Argentina.

14 ⁴Department of Plant and Wildlife Sciences, Brigham Young University (BYU), Provo,

15 UT, USA.

16 ⁵Biological and Environmental Sciences and Engineering Division, King Abdullah

17 University of Science and Technology (KAUST), Thuwal, Saudi Arabia

18 ⁶Facultad de Agronomía, Universidad de Buenos Aires and Instituto de Investigaciones

19 Fisiológicas y Ecológicas Vinculadas a la Agricultura (IFEVA-CONICET), Buenos

20 Aires, Argentina.

21

22 Correspondence should be addressed to Ramiro N. Curti,

23 Phone/fax number: +54 9 387 538-2092

24 Email: rcurti@agro.uba.ar

25 **Abstract**

26 Understanding how leaf morphology mediates plant responses to environmental
 27 variation is essential for predicting species adaptability under climate change. In this
 28 study, we investigated natural variation in leaf shape and associated functional–
 29 physiological traits (FPTs) across populations of *Chenopodium hircinum* grown in a
 30 common garden. We found that leaf shape strongly correlates with the climatic
 31 conditions of population provenance, while functional and physiological traits are
 32 independently associated with morphology rather than directly with climate. Landmark-
 33 based morphometric analysis revealed that the second principal component,
 34 distinguishing deeply lobed from rounded leaves, is significantly linked to key traits
 35 such as leaf mass per unit area (LMA) and stomatal conductance. These relationships
 36 suggest that morphology mediates a functional continuum between resource-use
 37 strategies. Notably, within-population phenotypic variation accounted for much of the
 38 observed trait diversity, underscoring the role of individual-level phenotypic plasticity
 39 in shaping ecological function. Our results challenge traditional views on the
 40 thermoregulatory role of leaf lobation and highlight morphology as a central axis of
 41 adaptation. This work advances understanding of trait integration in response to
 42 environmental heterogeneity and suggests that plasticity in leaf shape and function may
 43 enhance resilience of *C. hircinum* across its native range.

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45

46 **Introduction**

47 The functional significance of leaf shape remains a central topic in plant evolutionary
 48 ecology and ecophysiology (Niklas et al. 2023). The extraordinary diversity of leaf
 49 morphology among terrestrial plants—both across species and within individuals—
 50 represents a key evolutionary innovation (Ferris 2019; Nakayama 2024). As primary
 51 organs of carbon assimilation, leaves are subject to strong selective pressures (Niklas
 52 1999), shaping ecological strategies and evolutionary pathways (Niinemets 2020). This
 53 morphological variation facilitates plant adaptation to diverse habitats, particularly
 54 given the sessile nature of plants and the leaf’s critical role as the interface with the
 55 surrounding environment (Vogel 2009).

56 Recent studies of herbaceous species demonstrate that environmental
 57 variables—especially temperature—exert a strong influence on leaf shape at both
 58 interspecific and intraspecific levels (Mason and Donovan 2015; Giupponi 2020;
 59 Hightower et al. 2024; Singhal et al. 2025; Curti et al. 2025), mirroring patterns
 60 observed in other plant groups (Peppe et al. 2011; Royer et al. 2012; McKee et al.
 61 2019). Several of these investigations link morphological variation to climatic gradients
 62 and adaptive functional traits. For instance, in *Helianthus*, leaf shape was associated
 63 with traits supporting climatic adaptation at both inter- and intraspecific scales (Mason
 64 and Donovan 2015). Likewise, Giupponi (2020) found that intraspecific leaf shape
 65 variation in *Campanula elatinoidea* aligned with traits indicative of climatic adaptation.
 66 Most recently, Singhal et al. (2025) reported a latitudinal gradient in leaf shape linked to
 67 thermoregulatory capacity in *Ipomoea hederacea*.

68 Prior studies exploring the relationship between leaf morphology and
 69 environment have typically contrasted broad categories of leaf types—e.g., entire versus
 70 dentate or lobed versus unlobed—and related these to physiological functions such as

71 thermoregulation and water balance (Royer and Wilf 2006; Nicotra et al. 2011). Entire,
 72 large-surfaced leaves have often been linked with efficient **transpirational** cooling in
 73 warm climates (Nicotra et al. 2011; Singhal et al. 2025). Nonetheless, physiological
 74 trade-offs—such as differences in chlorophyll content—**remain largely species-specific**
 75 (Mason and Donovan 2015; Everingham et al. 2024), and temperature appears to exert
 76 limited effects on leaf mass per area (Niklas et al. 2023). **Importantly**, many herbaceous
 77 taxa exhibit substantial intraspecific variation in leaf shape that goes beyond binary
 78 classifications. In particular, lobed-leaf species may show variation in the number,
 79 depth, and position of lobes, as well as in their distribution along the lamina (Gupta et
 80 al. 2020; Balant et al. 2024; Hightower et al. 2024). This raises the question: can such
 81 subtle within-species variation in marginal complexity contribute to functional traits
 82 involved in thermal adaptation? **Focused** intraspecific analyses are needed to clarify the
 83 extent to which fine-scale morphological differences **mediate** physiological responses
 84 across environmental gradients.

85 A recent study assessed the utility of various leaf shape descriptors—including
 86 geometric morphometric approaches such as landmark- and outline-based analyses—in
 87 capturing morphological variation in *Chenopodium hircinum* (Curti et al. 2025), the
 88 **wild progenitor** of quinoa (*C. quinoa*) (Jarvis et al. 2017; Rey et al. 2023; Maughan et
 89 al. 2024). Native to South America, *C. hircinum* is **primarily** distributed in Argentina
 90 (Wilson 1990; Curti et al. 2023), where it is increasingly studied for traits that may
 91 confer climate resilience to quinoa (Curti et al. 2022; Agüero-Martínez et al. 2024; Curti
 92 et al. 2025; Xu et al. 2025). The species occurs across a broad elevational and thermal
 93 **gradient** in Argentina (Curti et al. 2023), and recent findings suggest that morpho-
 94 phenological and leaf-**shape** variation are **shaped more by individual and within-**
 95 **population differences than by broad ecoregional patterns** (Curti et al. 2022; Curti et al.

2025). Moreover, trait variation correlates with the east–west temperature gradient, suggesting a high degree of phenotypic integration (Curti et al. 2022; Curti et al. 2025).

In Argentinean populations of *C. hircinum*, geometric morphometric approaches outperformed traditional shape metrics (e.g., aspect ratio, circularity, solidity) in capturing leaf shape variation. Landmark and elliptical Fourier descriptors revealed clear population-level differentiation in lobulation patterns along the blade: basal lobulation predominates in high-elevation, colder sites, whereas mid-blade lobulation is more common in warmer, low-elevation populations (Curti et al. 2025). If such thermal gradients influence leaf morphology, populations across these gradients should also differ in physiological and functional traits. In addition, given the high morphological and physiological plasticity of ruderal species in general (Everingham et al. 2024; Hočevár et al. 2025), and of *C. hircinum* in particular (Curti et al. 2022; Curti et al. 2025), we hypothesize that leaf shape will more accurately predict physiological than functional trait variation. In this study, we address the following questions: Does variation in leaf lobulation influence physiological and functional traits independently? If so, is this influence primarily driven by species-level or individual-level variation?

Materials and Methods

Collection sites, common garden experiment and leaf sampling

This study analyzed seeds from 11 populations of *Chenopodium hircinum* collected within the Salta and Jujuy provinces of Northwest Argentina (Table S1). The majority of seeds originated from a recent collection undertaken during January and February of 2023, while seeds from two populations (LSK and SCA) were sourced from a collection in January 2022. The ecoregions represented by these seed origins are High Monte, Dry Chaco, and Central Andean Puna, in descending order of sample representation (Table S1). Mean summer temperature (MST, °C) and accumulated summer precipitation

121 (ASP, mm) data for the collection sites during the austral summer months (January to
122 March) were acquired from WorldClim (<https://www.worldclim.org/>) at a spatial
123 resolution of 30 arc-seconds (approximately 1 km² at the equator).

124 A common garden experiment was conducted ex situ between January and
125 March of 2024 at the Experimental Field of the National University of Salta (24.72° S,
126 65.41° W, 1228 m a.s.l.) under outdoor conditions. Seeds underwent a dormancy-
127 breaking protocol as described by Curti et al. (2022). Following germination in Petri
128 dishes (indicated by radicle emergence), seedlings were transplanted into 7-liter pots
129 arranged in a completely randomized design, with ten replicate pots per population. Pots
130 were filled with a 3:1 (v/v) mixture of sand and peat substrate, initially sown with five
131 plants per pot and subsequently thinned to a single plant. To mitigate potential edge
132 effects, pots were randomly repositioned every two days.

133 A total of 53 fully expanded leaves were sampled at the anthesis stage from
134 three to eight individual plants per population (Table S1). Specifically, leaves were
135 harvested from the middle third of the main stem of each plant, coinciding with the
136 location where physiological and functional traits were also assessed (see below). After
137 petiole excision, leaves were positioned adaxially on graph paper and photographed
138 using a digital camera (Nikon D7200, Nikon Corporation Hong Kong) at a consistent
139 distance. Images were saved as standard JPEG files for subsequent image analysis.

140 *Evaluation of leaf shape, physiological and functional traits*

141 Shape descriptors, including circularity (CIRC), aspect ratio (AR), and solidity, were
142 computed using ImageJ (<https://imagej.net/ij/>) following the conversion of leaf images
143 to binary silhouettes (Curti et al. 2025). Eight previously established landmarks on the
144 leaf outline of *C. hircinum* were digitized using the ImageJ point tool (Curti et al. 2025).

145 Additionally, Elliptical Fourier Descriptors (EFDs) were calculated according to the
146 methodology outlined in Curti et al. (2025).

147 Three physiological traits were measured on clear sunny days between 11:00 am
148 and 16:00 pm on previously irrigated pots at dawn. Measurements included stomatal
149 conductance (g_s , $\mu\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$) using a leaf porometer (SC-1 Meter Group USA
150 2021), chlorophyll concentration (CHL, $\mu\text{mol m}^{-2}$) using a MC-100 (Apogee
151 Instruments INC, USA), and leaf temperature ($^{\circ}\text{C}$, LTP) with an infrared thermometer
152 (GM320, China). Three functional traits were evaluated in the same leaves that were
153 used for physiological measurements. Leaf dry mass per unit area (mg mm^{-2} , LMA) was
154 determined by weighting leaves (discarding the petiole, LDW mg) and computing leaf
155 area (mm^{-2} , LA) from digitalized leaf image.

156 *Data analysis*

157 All statistical analyses were performed within the R environment (R Core Team, 2024).
158 Initial analyses involved a general description of leaf shape based on landmarks and leaf
159 outlines, following a previously published protocol (Curti et al. 2025). Briefly,
160 landmark coordinates were processed using the ‘shapes’ package (Dryden and Mardia
161 2016) after undergoing Generalized Procrustes Analysis (GPA). Subsequently, Principal
162 Component Analysis (PCA) was applied to the Procrustes-aligned coordinates, and
163 Principal Component (PC) scores for all retained components (hereafter, Ldk PCs) were
164 determined using the broken-stick model implemented in the ‘PCDimension’ package
165 (Wang et al. 2017). The analysis of leaf outlines followed a similar procedure:
166 coordinates of leaf silhouettes were acquired using the ‘Momocs’ package (Bonhomme
167 et al. 2014), and outlines were normalized via a full GPA adjustment based on the eight
168 previously defined landmarks. Following alignment, Elliptical Fourier Transforms were
169 fitted separately for the x and y coordinates. The number of harmonics to be retained for

subsequent analysis was estimated based on accumulated harmonic power (Bonhomme et al. 2014), and PC scores for the retained components (hereafter, EFD PCs) were extracted using the ‘PCDimension’ package.

The relationships among Functional and Physiological Traits (FPTs: LDW, LMA, LA g_s , LTP, and CHL), shape descriptors (CIRC, AR, solidity, retained Ldk PCs, and EFD PCs), and climatic conditions (Elevation, MST, and ASP) were assessed using Escoufier’s RV coefficients (‘FactoMineR’ package, (Josse et al. 2008; Lê et al. 2008)) with standardized variables. A Multivariate Multiple Regression (MMR) analysis (‘car’ package, (Fox et al. 2001)) was employed to test whether shape and climatic variables significantly predicted FPTs, utilizing a MANOVA (Pillai’s trace statistic). Subsequently, multiple linear regression (MLR) analyses were fitted to identify which predictor variables accounted for variation in each FPT individually. A second MMR analysis was conducted using significant predictor variables identified in the initial MLR analyses, again employing MANOVA with the Pillai statistic. Correspondingly, MLR analyses were performed to further examine the influence of these significant predictor variables on individual FPTs. A comparison between the full model (first MMR analysis) and the simplified model (second MMR analysis) was performed using an ANOVA. Finally, Redundancy Analysis (RDA) was performed using the ‘vegan’ package (Oksanen et al. 2001) to visualize the results of the best-fitting MMR model. The significance of the model, predictors (shape and climatic variables), and the number of RDA axes required to explain variation in FPTs were evaluated using a permutation test. A triplot displaying the relationships among the matrices of FPTs, samples, and predictors on the retained RDA axes was constructed for visual interpretation.

Results

General patterns of leaf shape variation

195 From the 16 Ldk PCs obtained, only the first two (Ldk PC1 and Ldk PC2) were
196 important to capture significant variation in leaf shape among samples (Fig. 1a). The
197 Ldk PC1 was associated with variations in the relative distances between landmarks 3
198 and 4, and 6 and 7, distinguishing leaves with pronounced lobulation in the middle
199 section from those with less lobulation in this region (Fig. 1a). In turn, the Ldk PC2
200 differentiated samples with deeply lobed leaves (trilobed) from those with rounded
201 leaves mainly associated with variation in landmarks 1, 2, 3, 4, 6, and 7 (all of them at
202 the central position along the leaf blade) (Fig. 1a).

203 Fourteen harmonics were necessary to describe leaf outlines (results not shown),
204 whereas only the first three Elliptical Fourier Descriptors PCs captured significant leaf
205 shape variation among samples (Fig. 1b). The EFD PC1 reflects overall leaf outline
206 variations, distinguishing samples with smoother and uniform contours (left) from
207 samples with irregular and wider shapes with an expanded base (Fig. 1b). The EFD PC2
208 captures changes in leaf area within the middle third, associated with an enlargement of
209 mild-lobing development, differentiating samples with deeply lobulation (trilobed) from
210 samples with rounded leaves (Fig. 1b). On the other hand, EFD PC3 was associated
211 with the development of lobes at the right side in middle-third along leaf blade (Fig.
212 1b).

213 *Interrelationships between shape, climate and FPTs*

214 A significant association was found between functional–physiological traits (FPTs) and
215 shape descriptors, as well as between shape and climate matrices; however, FPTs
216 showed no direct relationship with climate variables (Table 1a). A follow-up analysis,
217 separating functional and physiological traits and examining each category of shape
218 descriptors, yielded consistent results. Functional traits were significantly associated
219 with all shape descriptors, whereas physiological traits correlated only with landmark-

220 and Fourier-based measures (Table 1b). Notably, functional and physiological traits
221 were not interrelated. In contrast, all shape descriptors showed significant associations
222 with climate factors and with each other (Table 1b).

223 The full model of MMR analysis revealed that shape descriptors and climate
224 factors were significant to predict leaf FPTs (Pillai test statistics = 1.987, approx. $F_{(66, 246)} = 1.846$, $p = 0.00042$). The significant predictors variables were mainly Ldk PC2 for
225 most traits, and MST and aspect ratio plus Ldk PC2 for LTP (Fig. 2b, c, d, e). None
226 predictor variables explained variation in both traits LDW and CHL (Fig. 2a, b). The
227 second MMR analysis considering only MST, aspect ratio and Ldk PC2 predictors
228 variables was also significant (Pillai test statistics = 0.764, approx. $F_{(18, 138)} = 2.622$, $p =$
229 0.00083). The significant predictors variables were mainly aspect ratio and Ldk PC2 for
230 most traits (Fig. 2a, b, c, d, e, f). The comparison between full and reduced models was
231 significant (Pillai test statistics = 1.41, approx. $F_{(48, 246)} = 1.574$, $p = 0.014$), implying
232 that the reduced model considering only significant predictors was better to describe
233 variation in FPT.

235 The Redundancy Analysis (RDA) showed that shape and climatic variables
236 explain 21% of the variation in FPTs responses. The permutation test confirmed the
237 significance of the MMR reduced model, with only shape descriptors (aspect ratio and
238 Ldk PC2) contributing to FPTs variation (Table S2). Only the first RDA component
239 was significant (Table S2). In the triplot, LMA and g_s were positively associated with
240 aspect ratio and positioned above the origin, while LA and LTP were linked to Ldk PC2
241 and positioned below (Fig. 3). Samples distributed along the first RDA axis showed
242 strong admixture among populations (Fig. 3). CHL and MST were near the origin,
243 aligning with their low significance and poor predictive capacity for FPTs responses.

244 Discussion

245 The principal findings of this study are threefold: (1) leaf shape variation among *C.*
 246 *hircinum* populations correlates strongly with the climatic conditions of their
 247 provenance sites; (2) physiological and functional traits are independently associated
 248 with leaf morphology; and (3) a substantial proportion of field-observed variation arises
 249 from within-population phenotypic plasticity. These results underscore a robust
 250 association between leaf form, physiological–functional attributes, and local climate,
 251 suggesting that environmental heterogeneity is a key driver of the ecological relevance
 252 of leaf morphology in *Chenopodium hircinum*. Furthermore, the marked contribution of
 253 within-population phenotypic plasticity highlights a critical mechanism through which
 254 *C. hircinum* adapts to environmental variability.

255 The relationships among leaf shape, functional–physiological traits (FPTs), and
 256 climate reveal a morphology-mediated pathway linking climate to plant function. While
 257 significant correlations emerged between shape descriptors and both FPTs and climatic
 258 variables (Table 1a), direct associations between climate and either functional or
 259 physiological traits were absent (Table 1b). Additionally, although functional and
 260 physiological traits were each strongly associated with shape, they were not
 261 significantly correlated with one another (Table 1b). This pattern indicates that leaf
 262 morphology acts as an independent mediator between environmental factors and
 263 physiological function. Landmark-based analyses identified the second principal
 264 component (PC2) as the only axis significantly distinguishing deeply trilobed from
 265 rounded leaves (Fig. 1), with PC2 showing strong correlations with multiple FPTs
 266 (Table 1b), as evidenced by multivariate multiple regression (MMR) and multiple linear
 267 regression (MLR) analyses (Fig. 2).

268 Redundancy Analysis (RDA) of the best-fit MMR model revealed a significant
 269 co-localization of leaf mass per unit area (LMA) and stomatal conductance (g_s) (Fig. 3).

270 Elevated g_s was positively correlated with aspect ratio and negatively correlated with
271 both leaf temperature and lobation (i.e., lower PC2 scores), consistent with theoretical
272 expectations that lanceolate, entire-margined leaves operate at sub-ambient
273 temperatures via high transpiration (Nicotra et al. 2011; Singhal et al. 2025). However,
274 these results also challenge the hypothesized thermoregulatory role of lobation, as lobed
275 leaves exhibited higher temperatures despite comparable area (Fig. 3).

276 The spatial spread of samples along PC2 further showed that lobed leaves
277 extended beyond the morphological range of rounded ones (Fig. 1), complicating efforts
278 to test whether lobation reduces internal heat transfer distances (Nicotra et al. 2011).
279 Moreover, the observed positive correlation between g_s and LMA, coupled with a
280 negative correlation between leaf dry weight (LDW) and LMA (Fig. 3), suggests a
281 resource-acquisitive strategy in *C. hircinum*. This pattern aligns with broad global
282 trends (Wright et al. 2004) and mirrors findings in *Helianthus* species, where enhanced
283 gas exchange correlates with leaf shape at both intra- and interspecific levels (Mason
284 and Donovan 2015). Notably, our findings highlight a clear link between this resource-
285 use strategy and contrasting leaf shape configurations—an association that remains
286 underreported in prior studies of leaf form–function relationships.

287 Deeply lobed leaves (low PC2 scores) were also larger in area (LA) and had
288 higher dry mass (Fig. 3). An allometric analysis revealed a slope < 1 between these
289 traits (Fig. 4), consistent with the concept of diminishing returns in leaf mass investment
290 (Niklas et al. 2007). Yet, tissue bulk density (LMA)—a proxy for lamina stiffness—was
291 inversely related to LDW, suggesting it does not fully explain the increase in leaf mass.
292 This points to additional structural factors such as leaf thickness as potential
293 contributors to elevated LMA, a hypothesis meriting further investigation in *C.*
294 *hircinum* (Shi et al. 2024). This observation supports the idea that individual

295 components of complex traits can vary independently and respond at different rates to
296 environmental change (Niinemets 1999; Poorter et al. 2009).

297 A key insight from this study is the broad range of phenotypic variation in FPTs
298 observed within *C. hircinum* populations grown under common garden conditions. As
299 phenotypic variation under controlled environments does not inherently reflect
300 environmental influences (Niinemets 2020), future experiments should explore trait
301 expression across contrasting environments—e.g., across growing seasons or via
302 reciprocal transplants. Such approaches could help disentangle the roles of genetic
303 variation and plasticity in driving the observed trait diversity.

304 Our results indicate that functional and physiological traits varied independently,
305 yet exhibited complex interrelationships (Fig. 3). This is particularly relevant given the
306 broad environmental heterogeneity characterizing the species' native range (Curti et al.
307 2022, 2023, 2025). Importantly, our findings emphasize the individual-level nature of
308 trait variation, rather than strict ecotypic differentiation, paralleling results in other wild
309 species (Westerband et al. 2021; Chandler and Travers 2024). In light of climate
310 change, intra-population phenotypic plasticity emerges as a crucial mechanism by
311 which *C. hircinum* may track rapid environmental shifts. Our study identifies potential
312 pathways—particularly those mediated by leaf morphology—through which this
313 species may respond to changing climatic conditions across its geographic range.

314 **Conclusions**

315 This study reveals a robust, morphology-mediated linkage between climate, functional–
316 physiological traits (FPTs), and leaf shape in *Chenopodium hircinum*. Leaf morphology
317 emerged as a central integrator, independently connecting climatic variables with
318 physiological and functional trait expression. Notably, deeply lobed and rounded leaf
319 forms corresponded to distinct trait syndromes, suggesting divergent ecological

320 strategies within populations. Furthermore, the pronounced within-population variation
 321 observed under common garden conditions points to a substantial role for phenotypic
 322 plasticity in shaping trait expression. This plasticity, particularly at the individual level,
 323 may serve as a key mechanism for adaptive responsiveness across heterogeneous
 324 environments. In the context of rapid climate change, such intra-population plasticity
 325 could facilitate persistence and functional versatility across *C. hircinum*'s geographic
 326 range. Collectively, these findings underscore the ecological significance of leaf shape
 327 beyond its taxonomic utility and emphasize the importance of integrating morphological
 328 analyses into studies of trait–environment interactions. Future research incorporating
 329 experimental manipulations and multi-environment trials will be essential for
 330 disentangling the relative contributions of plasticity and genetic differentiation to trait
 331 variation in this widespread species.

332 **Supplementary data**

333 Table S1. Passport data of *Chenopodium hircinum* populations evaluated in the present
 334 study

335 Table S2. Redundancy analysis (RDA) results showing the significance of the
 336 simplified MMR model, associated climate factors and shape descriptors, and retained
 337 axes

338 **Acknowledgments**

339 **Conflict of interest**

340 The authors declare no conflict of interest.

341 **Data availability**

342 The data that support this study will be shared upon reasonable request to the
 343 corresponding author.

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469 Table 1. RV coefficients (below diagonal) and their significance (*p*-values, upper
470 diagonal) for the associations between Functional and Physiological Traits (FPTs),
471 Climate and Shape descriptors matrices on a general basis (a) and an individual basis
472 (b).

(a)						
	FPT		Climate		Shape	
FPT			0.51		$1.21e^{-06}$	
Climate	0.04				$3.66e^{-04}$	
Shape	0.26		0.19			
(b)						
	Funct ¹	Physl ¹	Clima ¹	Shape	Ldks ¹	EFDs ¹
Funct		0.17	0.24	0.01	$2.79e^{-7}$	$1.20e^{-4}$
Physl	0.07		0.84	0.11	0.01	0.10
Clima	0.02	0.01		$3.00e^{-3}$	$1.00e^{-3}$	$4.00e^{-3}$
Shape	0.12	0.08	0.15		$3.36e^{-8}$	$4.58e^{-12}$
Ldks	0.31	0.12	0.17	0.36		$5.97e^{-12}$
Outls	0.19	0.09	0.13	0.45	0.43	

474 ¹Funct: Functional; Physl: Physiological; Clima: Climate; Ldks: Landmarks; EFDs:
475 Elliptical Fourier Descriptors.

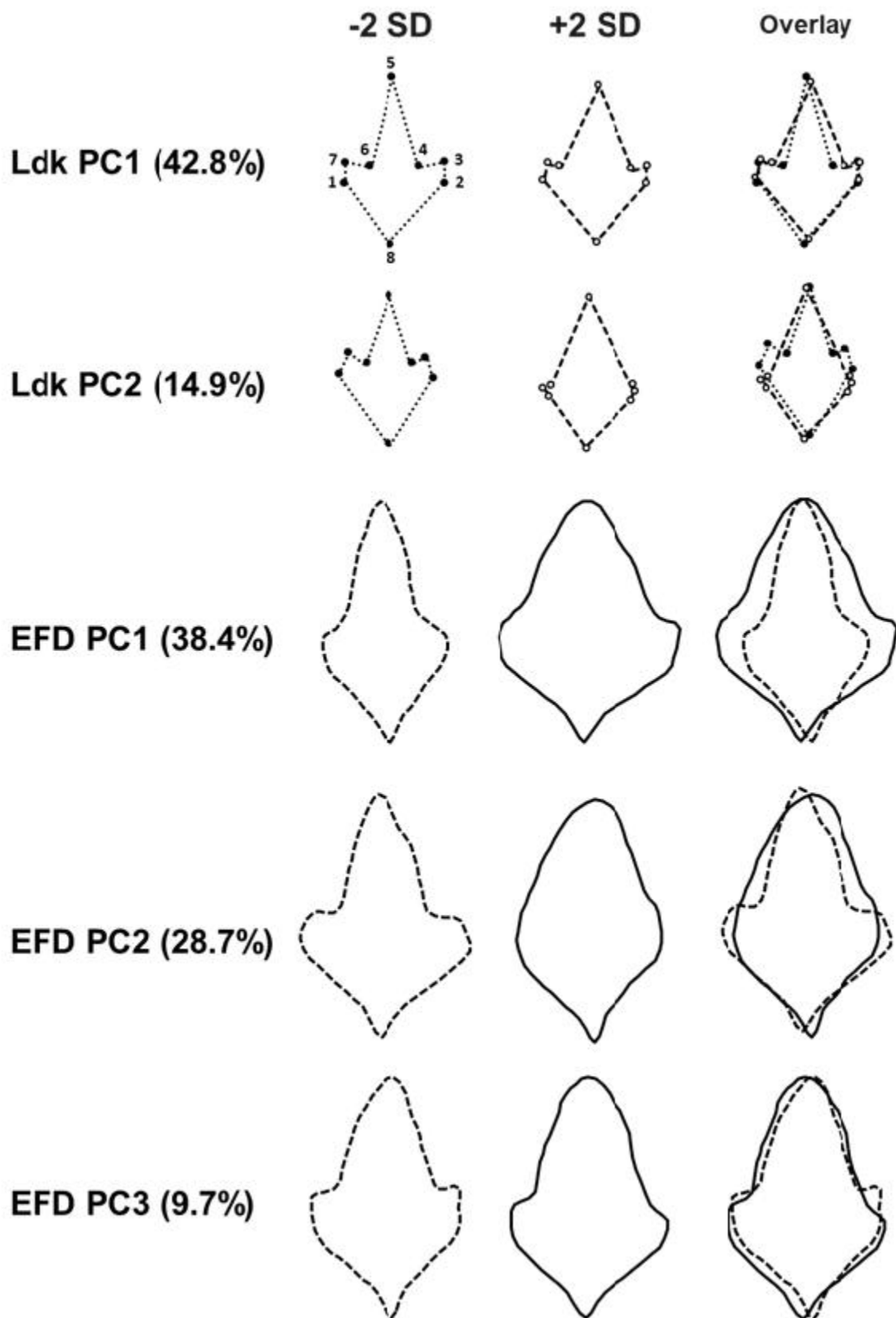
476 **Figure captions**

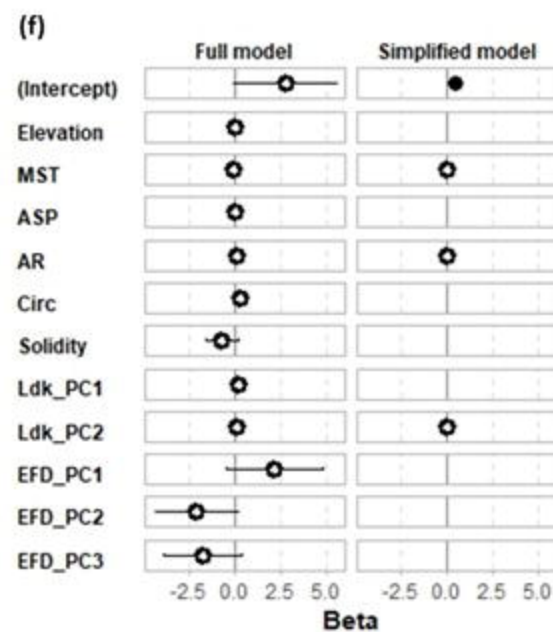
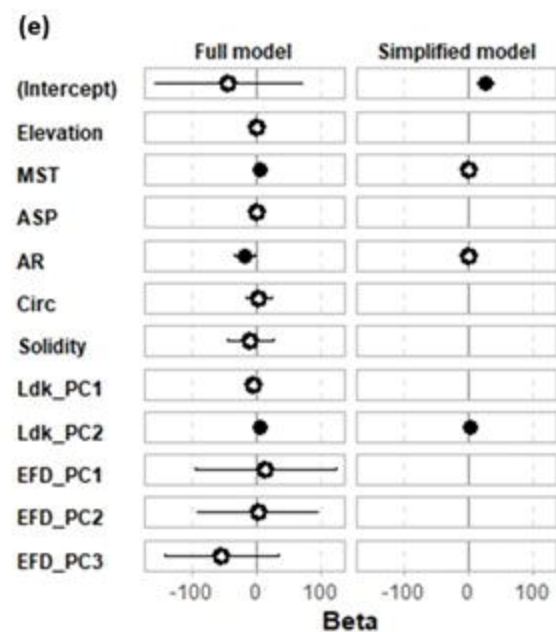
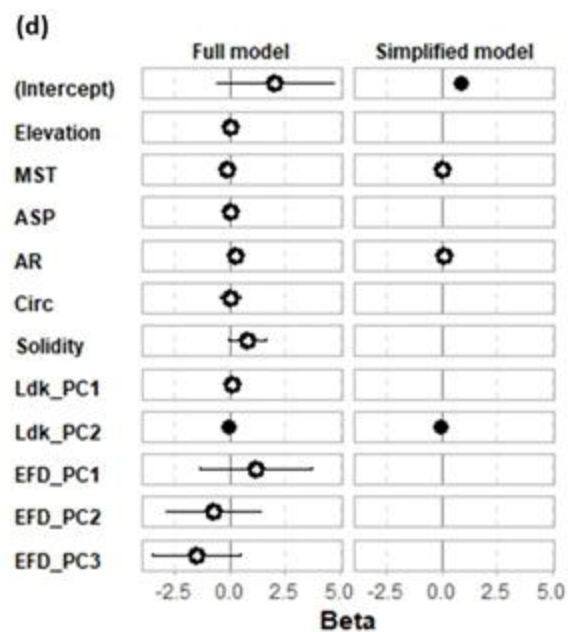
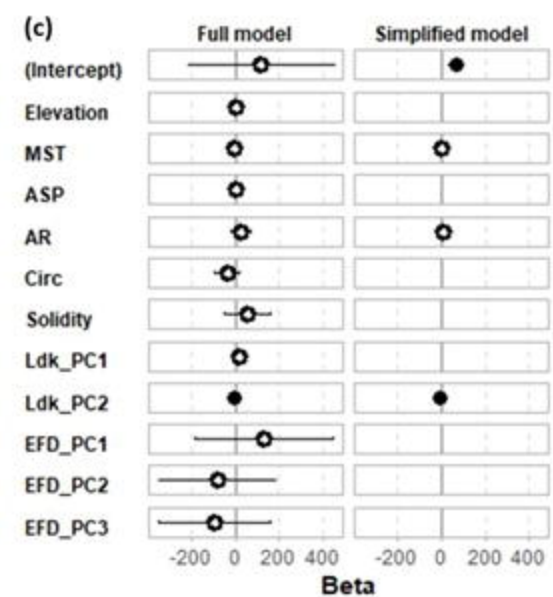
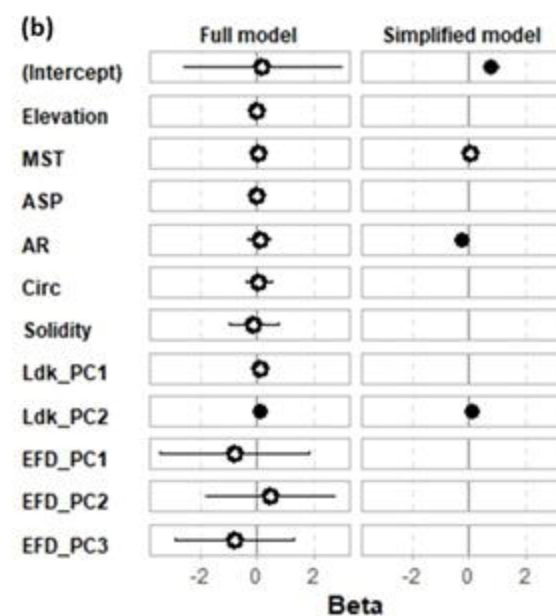
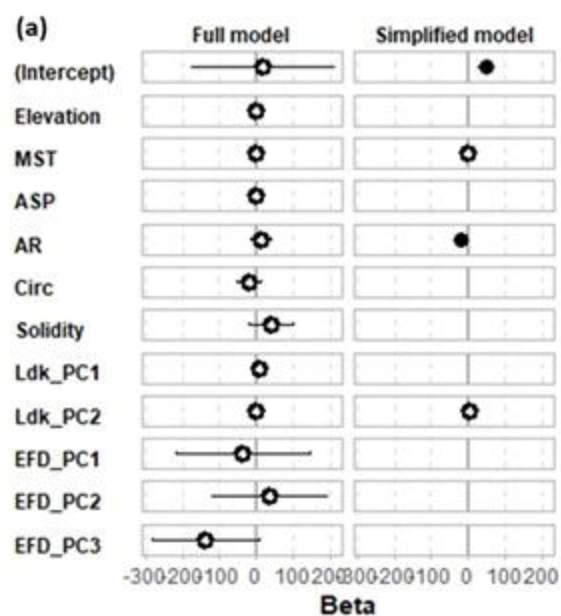
477 **Fig. 1** Principal components analyses (PCA) were performed using both landmark
 478 coordinates and Elliptical Fourier Descriptors (EFDs) to generate representative
 479 “eigenleaves” summarizing shape variation. For each principal component (PC) that
 480 significantly contributed to morphological variation, the proportion of explained
 481 variance is reported. Shape changes along each PC axis are visualized using
 482 reconstructed leaf outlines at ± 2 standard deviations (SD) from the mean—solid lines
 483 for -2 SD and dashed lines for $+2$ SD—demonstrating the extent of variation captured.
 484 Key shape differences are further emphasized by overlaying these opposing outlines.
 485 The positions of eight key morphological landmarks are also indicated.

486 **Fig. 2** Plots illustrating the coefficients of both the full and simplified models for (a)
 487 LDW, (b) LA, (c) LMA, (d) g_s , (e) LTP, and (f) CHL.

488 **Fig. 3** Triplot of the 1st component of RDA of *C. hircinum* samples, functional-
 489 physiological traits (responses) and attributes (predictors). Populations are displayed by
 490 symbols.

491 **Fig. 4** Log–log bivariate relationship for LA vs. LDW. Information about the regression
 492 model, coefficient of determination (R^2) and significance (p-value) are shown.





● $p \leq 0.05$ ○ $p > 0.05$

