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Original Article

Isolated but phenotypically similar: comparing oceanic island populations of the land crab *Johngarthia lagostoma*

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ABSTRACT

Restricted gene flow often leads to structured populations that may experience distinct selective pressures. Understanding the extent to which genetic and phenotypic variation are related can therefore reveal the evolutionary mechanisms shaping disconnected lineages. Oceanic island endemic taxa offer valuable opportunities for exploring this relationship, as they inhabit geographically isolated, usually geologically young, and environmentally stable systems where population genetic structure is strong. The yellow land crab *Johngarthia lagostoma*, restricted to South Atlantic islands, comprises three genetically distinct populations based on previous genetic study, yet little is known about its phenotypic variation. Here, we compared growth patterns and shapes of the carapace, abdomen, and chelipeds between populations from two equatorial islands (Rocas Atoll and Fernando de Noronha) and one subtropical island (Trindade). Chelar polymorphism was consistent across locations, with balanced frequencies between homochelous and heterochelous morphs. For all traits, we found overlaps in morphometric spaces among populations and structure-related selective pressures, without any match between genetic and phenotypic distances. Our findings are consistent with ancestral polymorphism retention and/or stabilizing selection acting on *J. lagostoma* populations as the processes underlying the observed patterns. These mechanisms are consistent with geological history and ecological homogeneity among islands, resulting in phenotypic similarity despite genetic divergence.

Keywords: evolution; natural selection; oceanic islands; Gecarcinidae; morphometry

INTRODUCTION

Since the 1980s, the field of phylogeography has greatly expanded our understanding of the microevolutionary processes operating at the population level across time and space (Avise *et al.* 1987, Beheregaray 2008, McGaughran 2015, Edwards *et al.* 2022). Many early phylogeographic studies were motivated by observations of phenotypic variation among populations (Zamudio *et al.* 2016). Over the past decades, extensive work has synthesized patterns of genetic structuring across thousands of taxa, revealing how landscape features, environmental conditions, and physical barriers shape lineage isolation (Beheregaray 2008, Edwards *et al.* 2022, McGaughran *et al.* 2022). With the development of high-throughput sequencing, we probably know more about genetic variation and its environmental correlates than about the phenotypic characteristics of isolated lineages (Edwards *et al.* 2015, Zamudio *et al.* 2016).

Linking genetic variability with phenotypic outcomes can help reveal, or at least suggest, the selective pressures acting across geographical and ecological contexts (Papadopoulou and Knowles 2016). Establishing genotype–phenotype associations in natural populations remains challenging. Yet, it provides a mechanistic framework for inferring evolutionary responses from past to present and anticipating potential future trajectories under environmental change (Zamudio *et al.* 2016). Assuming that populations share a similar ancestral phenotype, subsequent divergence or persistence of similarity may arise from habitat shifts, climatic variation, or biotic interactions such as predation and competition, each imposing distinct evolutionary scenarios (Losos 2011, Stayton 2015).

Population genetics theory predicts that geographically and genetically isolated populations are expected to diverge phenotypically over time (Gould and Johnston 1972, Warwick *et al.* 2015), whether through drift or divergent selection under contrasting local pressures (Endler 1973, Zamudio *et al.* 2016). In such cases, genetic and phenotypic structuring are expected to covary. However, isolation does not always coincide with phenotypic differentiation (Lande 1980), raising questions about the persistence of similarity among populations (Cerca 2023).

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Phenotypic similarity can arise neutrally through drift or from the retention of ancestral polymorphism (Stayton 2015, Magalhaes *et al.* 2015). Conversely, when comparable selective conditions operate independently across localities, populations may evolve similar traits, a process known as parallel evolution (Bolnick *et al.* 2018, De Lisle and Bolnick 2020). Finally, when populations inhabit relatively stable and homogeneous environments over space and time, phenotypic variation among lineages may remain subtle or cryptic, as expected under stabilizing selection (Nourmohammad *et al.* 2013, Reilly and Wake 2015, Punzalan and Rowe 2016, Zamudio *et al.* 2016).

Understanding which of these processes—divergence, parallelism, or stabilization—prevails in natural systems requires models in which ecological and evolutionary factors can be clearly disentangled. Oceanic islands provide such natural laboratories, where ecological conditions, spatial barriers, and colonization history jointly drive evolutionary trajectories (Whittaker 1998, Losos and Ricklefs 2009, Paulay and Starmer 2011). Island systems are geographically isolated; thus, species often experience strong genetic drift, founder effects, and localized selection pressures, resulting in rapid evolutionary change (Losos and Ricklefs 2009). Yet, their relative simplicity, low diversity, high endemism, and reduced predation and competition (Pinheiro *et al.* 2017) can also promote ecological stability over time. Many oceanic islands are geologically young, arising without pre-existing biota, so the evolutionary differentiation of endemic lineages may have occurred over relatively short timescales (Wang *et al.* 2014). Moreover, dispersal among islands is limited by well-defined physical barriers such as oceanic distance and current systems (Wang *et al.* 2014, Freire *et al.* 2021, Gyllenhaal *et al.* 2025), providing a framework for examining how ecological isolation shapes phenotypic evolution.

Among island-endemic taxa, land crabs (families Coenobitidae and Gecarcinidae) are striking examples of how ecological and evolutionary processes interact in insular environments (Paulay and Starmer 2011). Although globally distributed, each species is typically restricted to a small group of islands (Perger *et al.* 2013, Laidre 2018, Perger 2019). On land, they occupy diverse habitats, with few or no native predators, often being the most abundant arthropods and functioning as keystone species within island ecosystems (Lindquist *et al.* 2009, Paulay and Starmer 2011, Perger 2014, Andrades *et al.* 2019). Adult individuals undertake conspicuous reproductive migrations from inland habitats to the coast (Hicks 1985, Burggren and McMahon 1988, Hartnoll *et al.* 2014, João *et al.* 2024a), releasing planktonic larvae that depend on ocean currents for dispersal (Rodríguez-Rey *et al.* 2016, Freire *et al.* 2021).

In the South Equatorial Atlantic, the yellow land crab *Johngarthia lagostoma* (H. Milne Edwards, 1837) is an endangered terrestrial species (Pinheiro *et al.* 2016, Cumberlidge and Sharp 2025) restricted to four oceanic islands (Hartnoll *et al.* 2006b, Tavares and Mendona 2022): Rocas Atoll (RA: 3°50’S) and Fernando de Noronha (FN: 3°50’S), both near the Brazilian coast; and Ascension (AS: 7°57’S) and Trindade (TR: 20°30’S), located farther offshore. These islands are volcanic and relatively young—approximately 12.5 Mya (FN), 3.7 Mya (TR), and 1.5 Mya (AS)—whereas the reef structure of RA dates to ~6 kya, reflecting a recent biogenic phase over an older volcanic base (Kikuchi and Leão 1997, Hartnoll *et al.* 2006b, Hachich *et al.* 2015, Freire *et al.* 2021). Oceanic currents among them vary in direction and intensity, potentially influencing larval dispersal and population connectivity (Mansfield *et al.* 2017, Freire *et al.* 2021).

Johngarthia lagostoma exhibits remarkable morphological variability within the islands. For AS and TR, previous studies have reported marked sexual dimorphism, polymorphism in cheliped morphology, and diverse coloration patterns (Hartnoll *et al.* 2009, 2017, João *et al.* 2022, 2023, 2024a). Despite the evidence of genetic discontinuity between three populations, (i) RA + FN, (ii) AS, and (ii) TR, based on a mtDNA marker (Rodríguez-Rey *et al.* 2016), available studies have so far described phenotypic variation only at the within-island level (Teixeira 1996, Hartnoll *et al.* 2009, João *et al.* 2022, 2024a), and no comparisons among islands or populations have yet been made.

Considering the geographical isolation and genetic structure of *J. lagostoma* across the South Atlantic islands, we investigated phenotypic variation among populations. Focusing on the populations from the Brazilian islands (RA + FN and TR), we measured growth patterns and shapes of the carapace, abdomen, and chelae, described within-population phenotypic variation for each structure, and compared overall patterns among populations to test three hypotheses based on evolutionary mechanisms. Our first hypothesis (H_1) assumes divergent selection, which predicts contrasting phenotypic patterns across populations. Alternatively, we tested the hypothesis of ancestral polymorphism or parallel adaptation (H_2), which predicts phenotypic polymorphism shared among genetically contrasting populations. Lastly, we tested the hypothesis of stabilizing selection (H_3), which predicts cryptic or undetectable phenotypic variation among geographical locations and/or populations.

MATERIAL AND METHODS

Study islands, sampling, and morphometric measurement

We sampled individuals in 2024 on three out of the four islands where *J. lagostoma* occurs (Fig. 1A): Rocas Atoll (RA: 3°51’S, 33°48’W), within the Cyperaceae vegetation of Farol Island; Fernando de Noronha (FN: 3°51’S, 32°26’W), in the forest associated with Sancho Beach; and Trindade Island (TR: 20°30’S, 29°20’W), in the sandhill vegetation of Andradas Beach. Rocas Atoll is the only atoll in the Atlantic Ocean, situated 266 km off the north-eastern coast of Brazil, a non-entry Marine Protected Area covering 7.5 km^2 (Kikuchi and Leão 1997). Geographically close to AR, Fernando de Noronha is the main island of the archipelago bearing the same name, located 360 km off the north-eastern coast of Brazil, with an emergent area of 18.4 km^2 (Grillo and Mello 2021), where tourism and permanent human residence are allowed (IBGE 2024). Finally, as part of the Trindade and Martim Vaz archipelago, Trindade Island is the southernmost Brazilian oceanic island, with an area of 13.5 km^2, located 1200 km off the south-eastern coast of Brazil (Schaefer and Oliveira 2015, Clemente *et al.* 2018). It is inhabited by approximately 40 people, including researchers and military personnel (PROTRINDADE 2018).

On all three islands, under permit ICMBio/SISBIO no. 91625-6, sampling was conducted at night, following the same design on each island and depending on the activity status of

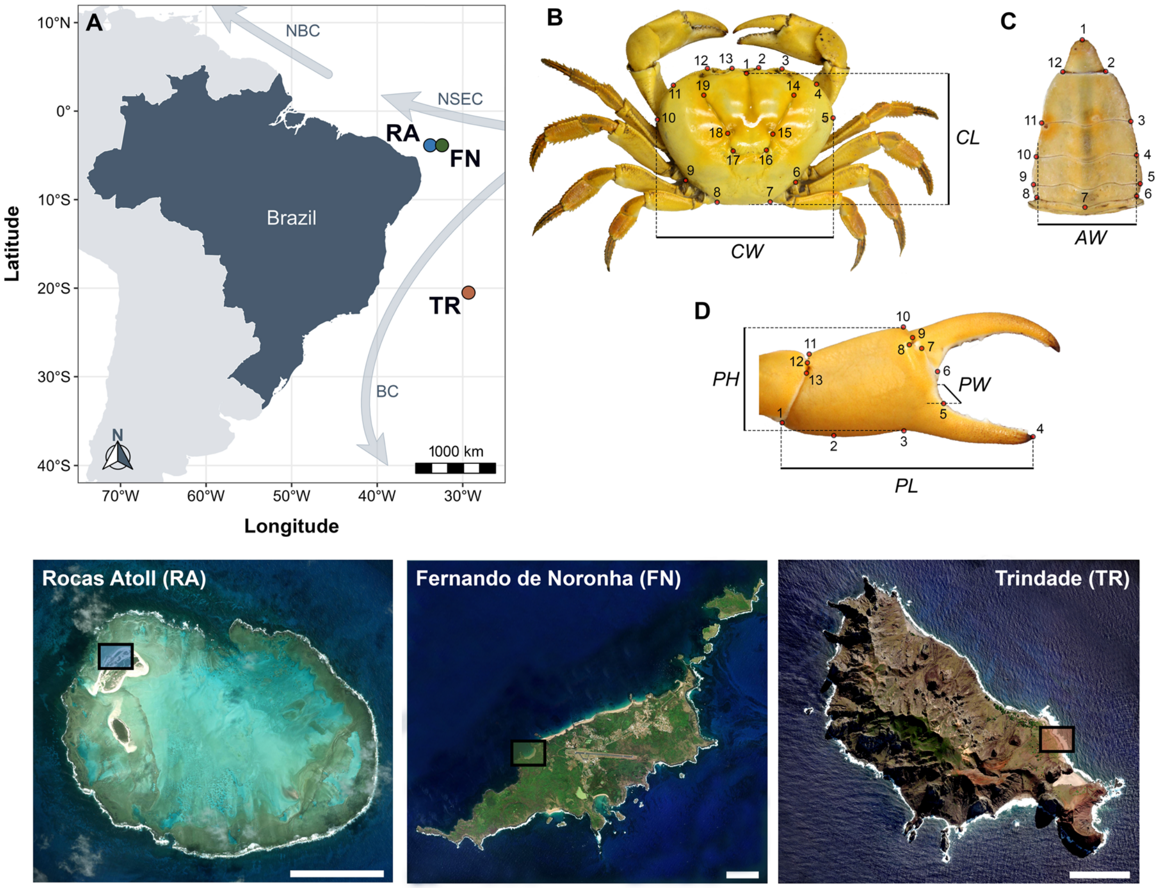

Figure 1. A, General overview of the three sampling sites for *Johngarthia lagostoma*, showing the main oceanic current systems that influence each island and the geographical position of Rocas Atoll (RA), Fernando de Noronha (FN), and Trindade Island (TR). B–D, Structures used for morphometric comparisons, highlighting linear measurements (black lines) and landmark positions (red dots) on the carapace (B), abdomen (C), and chelae (D). Below: satellite images showing the landscape of RA, FN, and TR, respectively (white scale bar = 1 km). AW, abdomen width; BC, Brazilian Current; CL, carapace length; CW, carapace width; NBC, North Brazilian Current; NSEC, North–South Equatorial Current; PH, propodus height; PL, propodus length; PW, propodus width.

J. lagostoma individuals. To sample active individuals associated with local vegetation, we established five to 10 transects of 10 × 3 m (30 m^2) parallel to the shoreline and at least 20 m apart to avoid sampling dependence. Within each transect, all active individuals were manually collected. In the absence of active crabs, we applied a random active search for burrows and captured the crabs by hand in the same vegetated area. Because burrow entrances were disturbed during hand-by-hand inspection, resampling was avoided. After collection, individuals were kept in labelled bags until sunrise to prevent resampling before measurements.

In the field, all individuals were sexed based on abdominal dimorphism (sub-triangular in males and semi-oval in females) and the number of pleopods (two pairs in males and four pairs in females). Using a digital caliper (precision 0.01 mm), we measured carapace width (CW, a proxy for body size), carapace length (CL), abdomen width (AW), and the propodus of both chelipeds (PL, propodus length; PH, propodus height; and PW, propodus width) (Fig. 1B–D). Using the cheliped measurements, we calculated the Chelar Mass Index ($CMI = PL \times PH \times PW$) for each cheliped, corresponding to chelar volume (Oka *et al.* 2016). After each male individual was measured, the dorsal and ventral carapace views and the external faces of both chelipeds were carefully cleaned and photographed at a fixed distance (50 cm) under natural light conditions to perform geometric morphometric analyses (see below). All photographs were taken with the same digital camera (Canon Rebel T7 with an 18–55 mm lens), including a millimetre scale, and with fixed aperture settings to avoid perspective errors (Supporting Information, Fig. S1).

For downstream analysis, only adult individuals were used ($CW \geq 57.9$ and 56.6 mm for males and females, respectively, following João *et al.* 2022) to avoid ontogenetic differences. Following previous descriptions of chelar polymorphism in *J. lagostoma* (Hartnoll *et al.* 2017, João *et al.* 2024a), individuals of both sexes were classified as homochelous (both chelae similar in shape and size) or heterochelous (chelae dissimilar in shape and/or size). Finally, individuals with broken or missing structures were excluded from analyses. All data processing and analysis were performed in the R environment (R Core Team 2024), as described below.

Linear morphometry comparison

To quantitatively assess the morphology of *J. lagostoma*, we employed a linear morphometric framework. We first applied a Principal Components Analysis (PCA) to all recorded variables to explore the linear morphometric space, grouping individuals by sex and by island within sexes. We also calculated the Variance Inflation Factor (*VIF*) to identify and exclude collinear variables ($VIF > 10$ indicates high collinearity; Kutner *et al.* 2004), retaining only those with higher explanatory power and representativeness for each body region or structure (i.e. carapace, abdomen, and cheliped). Subsequently, we used *CL*, *AW*, major *CMI* (volume of the major chela), and *CMI* sum (sum of the volumes of both chelae) as response variables.

To contrast linear morphometry among individuals from each island, we used CW as the reference for body size and as covariate, focusing on the growth patterns of each response variable rather than on body size effects. To interpret the growth pattern of each response variable, we applied regression analysis with fit by power-function ($Y = a\ X^b$), conducted separately for each island (RA, FN, and TR), sex (males and females), and chelar morphotype (for chelar variables). All variables were log-transformed to reveal growth patterns, which were evaluated by the slope (b) (Hartnoll 1982). Each relationship was classified as isometric ($b = 1$), positively allometric ($b > 1$), or negatively allometric ($b < 1$). The reference value was 1 for CL and AW relationships, and 3 for chelar–volume relationships, owing to their cubic nature (Huxley 1932, Shingleton 2010). Departures from isometry ($b \neq 1$ or $b \neq 3$) were tested using a Student's *t*-test (Sokal and Rohlf 2012).

Finally, to test contrasts in growth patterns, we applied Analysis of Covariance (ANCOVA; Sokal and Rohlf 2012). Differences among factor levels (sexes and islands) would be unveiled when the interaction between the covariate and factors was significant, indicating differences in the models' slopes. To avoid the effects of sexual dimorphism in comparisons, we first applied models with sex as a factor and, if differences were not rejected, we then applied separate models for each sex to contrast among islands. Additionally, for chelar variables, we also used chelar morphotype as a factor. When differences were not rejected by ANCOVAs, we applied post hoc tests using the *emtrends* function from the *emmeans* package v.1.10.0 (Lenth 2024) to contrast the adjusted models.

Geometric morphometry comparison

Due to the sensitivity of the data, only males were used for geometric morphometric comparisons to avoid confounding sexual dimorphism with inter-island differences. Females were therefore excluded from all geometric morphometric analyses. Consequently, all shape-based inferences presented here refer exclusively to males and should not be interpreted as extending to female morphometry. We used tpsDig2 software (v.2.32, Rohlf 2021) to digitize two-dimensional landmarks for the carapace ($N = 19$), abdomen ($N = 12$), and each chela ($N = 13$) (Fig. 1B–D). The same person digitized all landmarks to minimize measurement error, and we tested landmark placement consistency in a subset of 20 individuals per structure.

With the raw landmark coordinates for each structure, we applied the subsequent steps and functions in the *geomorph* package (Adams *et al.* 2025). First, we performed a Generalized Procrustes Analysis (GPA) using the *gpagen* function, which controls for errors in landmark digitization and object position, orientation, and scale. We superimposed all objects in a common coordinate system (Adams *et al.* 2004), removing non-shape information (Rohlf and Slice 1990). We obtained the centroid size of each structure per individual as a proxy for structure size. We used it as a covariate in shape comparisons among islands to control individual size effects.

To test for shape differences of each structure among islands, we used the *procD.lm* function, which performs Procrustes-based linear models with permutation procedures. This approach was conceptually equivalent to a Multivariate Analysis of Covariance (MANCOVA), since centroid size was included as a covariate and the Procrustes coordinates as the multivariate response variable (adapted from Rosenberg 1997). For the carapace and abdomen, models considered only islands as a factor. For chela shape, the model incorporated individual identity as a random effect and included chela number (one or two, assigned randomly), chelar morphotype (*HO* or *HE*), and island as fixed factors. As in linear morphometric analyses, when a significant effect of centroid size was detected, we considered only shape differences supported by a significant interaction between centroid size and the factors. Additionally, we applied post hoc pairwise tests using the *pairwise* function to examine group contrasts. Finally, we extracted model residuals and used them to perform Canonical Variates Analysis (CVA) to visualize shape differences.

Association between morphometric and genetic distances

After completing both linear and geometric morphometric analyses, we extracted distance metrics to test their association with the population genetic distances (F_{ST} and Φ_{ST}) based on concatenated partial sequences of *COI* and 16S genes previously reported by Rodríguez-Rey *et al.* (2016). For this purpose, we considered only male individuals to calculate distances for each structure (carapace, abdomen, and chela). For the linear morphometric dataset, we generated distance matrices by quantifying pairwise dissimilarities among islands based on the Euclidean distance between slope coefficients of the log–log models. For the geometric morphometric dataset, we used Procrustes-aligned landmark configurations to compute pairwise Mahalanobis distances among islands.

We then tested the association between the two morphometric approaches using Mantel tests (Mantel 1967), with 999 permutations, using Pearson's correlation between matrices. To further investigate the relationship between morphometry and genetics, we applied the same procedure, correlating the genetic-distance matrix with both morphometric-distance matrices. Given the strong correlation between linear and geometric morphometry (see Results), subsequent associations with genetic distances were primarily based on Mahalanobis distances, as these better reflect overall structural variation. Due to the number of islands (three), the number of pairwise distances available for the Mantel test is quite limited. Consequently, statistical significance cannot be robustly assessed, and results were interpreted as descriptive trends based on Pearson coefficients rather than a formal correlation test.

RESULTS

We sampled 378 adult individuals across the three islands. At RA, we captured 83 males and 76 females, with CW ranging from 57.7 to 97.2 mm (mean ± SD: males, 81.1 ± 9.3 mm; females, 75.4 ± 7.3 mm). At FN, we obtained 67 males and 33 females, with CW varying from 67.9 to 104.7 mm (males, 89.8 ± 7.4 mm; females, 83.1 ± 6.1 mm). At TR, we sampled 89 males and 30 females, with CW ranging from 61.5 to 103.8 mm (males: 86.0 ± 9.7 mm; females: 78.5 ± 7.5 mm). Both chelar morphotypes were recorded on all islands and in both sexes. In males, the frequency of morphotypes was balanced (HE, *N* = 122, 51.3%; HO, *N* = 116, 48.7%), whereas in females, they were predominantly HO (*N* = 104, 76.5%).

Linear morphometric comparison

In linear morphometric space, sex explained more variability than island (Fig. 2). Among variables, only *AW* showed low collinearity (*VIF* = 2.7), whereas the others were highly collinear (*VIF* > 10). Therefore, we retained one representative variable per structure (*CW*, *AW*, and *CMI Sum*) for PCA. In the PCA considering both sexes, the first two principal components (PCs) explained 98.1% of morphometric variation, largely reflecting sexual dimorphism, with PC1 and PC2 capturing within- and between-sex variation, respectively (Fig. 2A). The *AW* variable explained most of the variation between sexes (85.4%). Separate PCAs for each sex revealed strong morphometric overlap among islands (Fig. 2B–C). For both sexes, PC1 explained more than 93.1% of the variability,

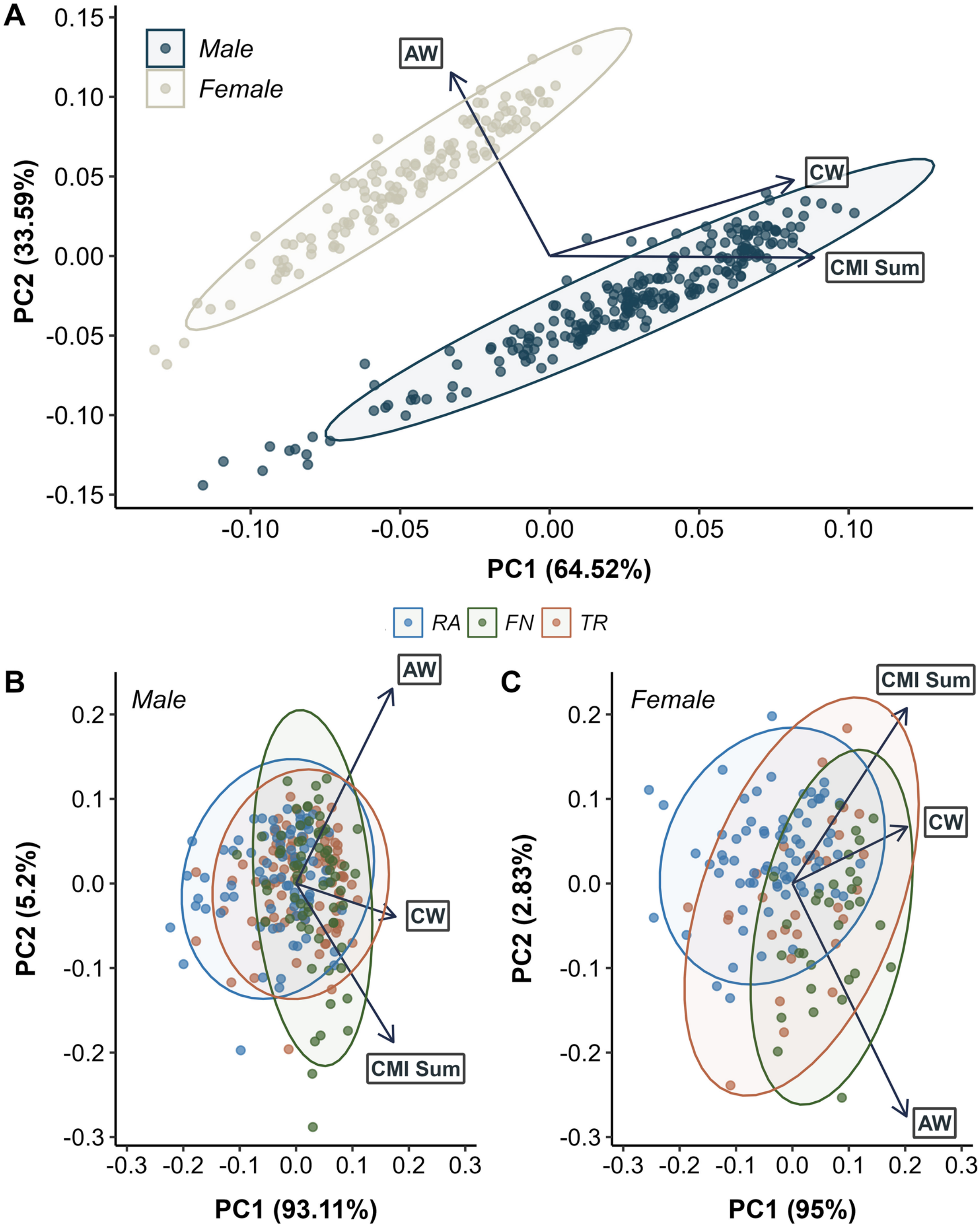

Figure 2. Variation in linear morphometrics of *Johngarthia lagostoma* from the three oceanic islands (RA, Rocas Atoll; FN, Fernando de Noronha; TR, Trindade Island), assessed by Principal Component Analysis (PCA) according to sex (A) and island within each sex shown separately for males (B) and females (C). AW, abdomen width; CW, carapace width; and CMI Sum, sum of the chela mass index of both chelipeds.

with all three variables contributing proportionally. All linear relationships between response variables and *CW* were positive and most showed good fit ($R^2 \geq 0.7$, $P < .05$), except those with small sample sizes (Supporting Information, Table S1). Across islands, relationships were highly consistent.

Each morphometric relationship followed a clear allometric trend; however, ANCOVA results indicated no significant pairwise differences among islands (Tables 1–2). For *CL* ~ *CW*, individuals from all islands showed a negative allometry ($b < 1$), with similar slopes between sexes (Fig. 3A). For *AW* ~ *CW*, males exhibited negative allometry ($b < 1$), whereas females showed isometry ($b = 1$) or positive allometry ($b > 1$) (Fig. 3B). For both chelar relationships (*major CMI* ~ *CW* and *CMI Sum* ~ *CW*) both sexes showed positive allometry ($b > 3$), but with steeper slopes in males than in females. No significant differences in chelar growth were evidenced between morphotypes within sexes; therefore, we pooled morphotypes and presented *CMI Sum* results to illustrate the overall variability in chela growth (Fig. 3C).

Overall, these results indicate that sexual dimorphism primarily regulates linear morphometric variation, especially in the abdomen and chelae, with high similarity among islands.

Table 1. Summary of the ANCOVA model testing the effects of the covariate (CW, carapace width) and the factors (Sex and Island) on the carapace length (CL) of *Johngarthia lagostoma*

Response variable	Source of variation	*d.f.*[a]	*MS*[b]	*F*[c]
CL	CW	1	4.04	16730.91*
	Sex	1	0.001	4.69*
	Island	2	0.05	212.43*
	Sex * Island	2	0.002	6.55*
	CW * Sex	1	0.0001	0.51[ns]
	CW * Island	2	0.001	4.36*
	CW * Sex * Island	2	0.000	0.07[ns]
	Residuals	366	0.0002	

[a] *d.f.*, degrees of freedom. [b] *MS*, mean-squares. [c] *F*, *F*-value.
*, significant p-value (p < 0.05). [ns], non-significant p-value (p > 0.05).

Geometric morphometry comparison

We detected a significant effect of centroid size on the shapes of the carapace, abdomen, and chelae (Table 3). All results in this section describe inter-island patterns only for males' individuals. For the carapace and abdomen, the interaction between centroid size and island was significant in the MANCOVAs; however, this effect was not sufficient to generate significant pairwise differences among islands for either structure. For chela shape, we did not detect significant effects of island or chelar morphotype (Table 3).

Despite the overall similarity, the geometric morphometric spaces of each structure suggested subtle trends among islands (Fig. 4). For the carapace, the first canonical axis explained 82.6% of the shape variation, with FN individuals showing relatively wider carapaces compared to RA and TR (Figs 1B, 4A, D). For the abdomen, the first canonical axis explained 85.1% of the variation, but with extensive overlap among islands (Fig. 4B), and TR individuals showed a slight tendency towards relatively longer abdomens (Figs 1C, 4E). For the chelae, the first canonical axis explained 69.8% of the variation and revealed strong overlap among islands (Fig. 4C). However, RA individuals displayed

Table 2. Summary of three ANCOVA models testing the effects of the covariate (CW, carapace width) and the factors (Island and Chelar Morphotype, CM) on the response variables (AW, abdomen width; Major CMI, major chela mass index; CMI Sum, sum of the CMI of both chelipeds) for males and females of *Johngarthia lagostoma*

Response variable	Source of variation	Males			Females		
		d.f.[a]	*MS*[b]	*F*[c]	*d.f.*	*MS*	*F*
AW	CW	1	2.34	1783.87*	1	2.02	1541.99*
	Island	2	0.009	7.22*	2	0.08	59.72*
	CW * Island	2	0.0001	0.09[ns]	2	0.004	3.02[ns]
	Residuals	233	0.001		132	0.001	
Major CMI	CW	1	81.80	2153.16*	1	17.69	1068.62*
	Island	2	0.37	9.84*	2	0.15	9.21*
	CM	1	2.08	54.66*	1	0.007	0.41[ns]
	Island * CM	2	0.19	5.00*	2	0.04	2.60[ns]
	CW * Island	2	0.05	1.25[ns]	2	0.02	1.42[ns]
	CW * CM	1	0.03	0.70[ns]	1	0.009	0.51[ns]
	CW * Island * CM	2	0.003	0.09[ns]	2	0.003	0.15[ns]
	Residuals	213	0.04		121	0.02	
CMI Sum	CW	1	72.49	1867.59*	1	17.08	734.45*
	Island	2	0.22	5.68*	2	0.13	5.64*
	CM	1	0.07	1.71[ns]	1	0.62	26.72*
	Island * CM	2	0.19	5.00*	2	0.11	4.86*
	CW * Island	2	0.07	1.77[ns]	2	0.03	0.58[ns]
	CW * CM	1	0.006	0.15[ns]	1	0.01	0.60[ns]
	CW * Island * CM	2	0.007	0.18[ns]	2	0.0002	0.008[ns]
	Residuals	213	0.004		122	2.84	

[a] *d.f.*, degrees of freedom. [b] *MS*, mean-squares. [c] *F*, *F*-value. *, significant p-value (p < 0.05). [ns], non-significant p-value (p > 0.05).

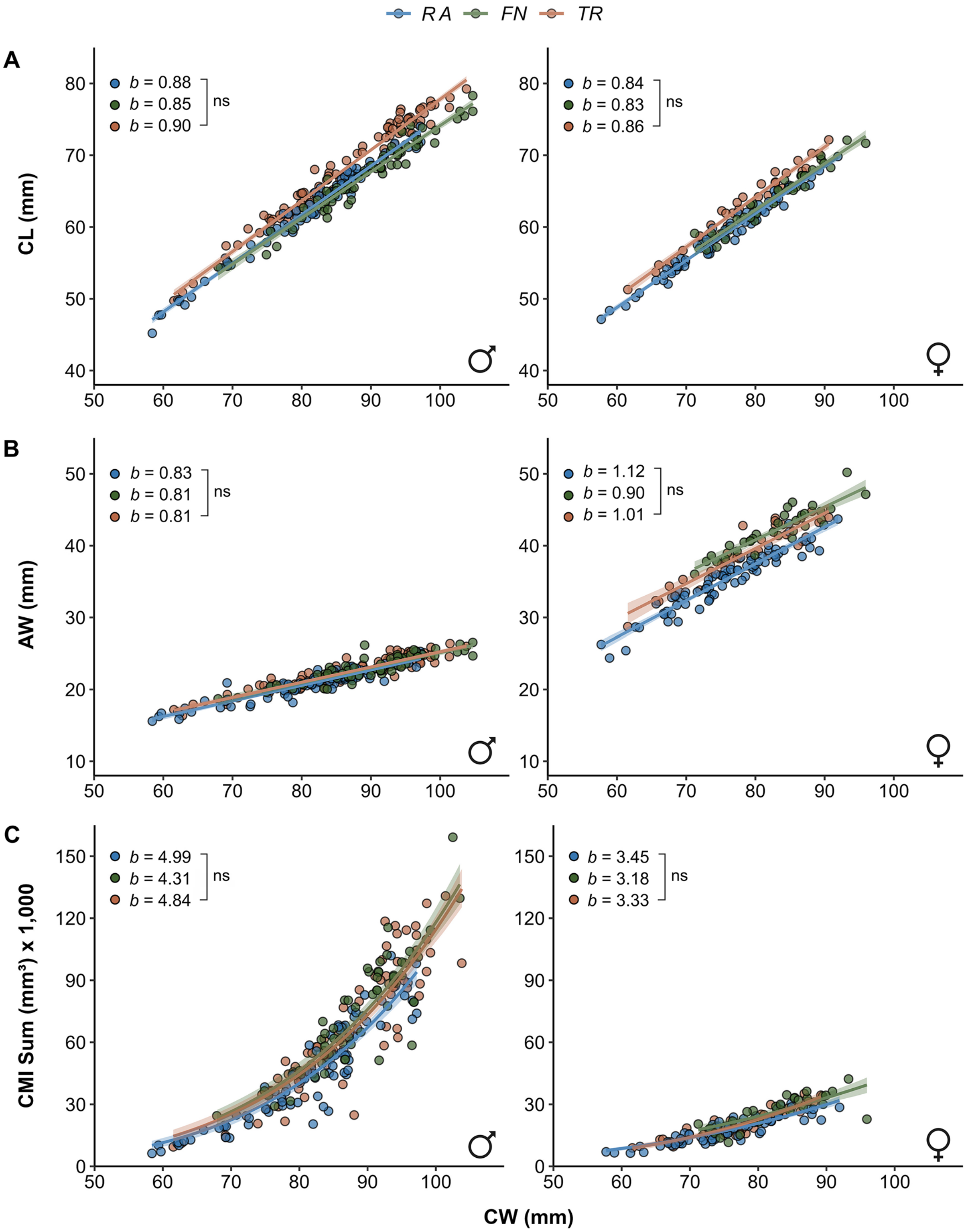

Figure 3. Linear morphometric relationships fitted to power functions ($Y = aX^b$) using carapace length (A), abdomen width (B), and sum of the chela mass index of both chelipeds (C) as response variables in relation to carapace width, for males and females of *Johngarthia lagostoma* sampled on the three oceanic islands (RA, Rocas Atoll; FN, Fernando de Noronha; TR, Trindade Island). AW, abdomen width; *b*, slope value of the estimated models; CL, carapace length; CMI Sum, sum of the chela mass index of both chelipeds; CW, carapace width; and ns, non-significant comparison of *b* values between islands within sexes.

subtle variation. Overall, regardless of structure, we observed only slight variation in geometric morphometric space among islands.

Association between morphometric and genetic distances

Both Euclidean and Mahalanobis distances revealed comparable patterns among islands (Table 4), showing a strong positive association across all structures ($r \geq 0.95$). Despite the overall concordance, each structure displayed a different island as relatively more distant from the others: FN for the carapace, TR for the abdomen, and RA for the chelae. Associations of Mahalanobis distances with genetic structure (Table 4D) varied by trait: no correlation for the carapace ($r = -0.05$), a strong positive

Table 3. Summary of three MANCOVA models testing the effects of the covariate (CS, centroid size) and the factors (Island, Chelar Morphotype, and Chela) on the shape of each structure (carapace, abdomen, and chela) for *Johngarthia lagostoma*

Structure	**Source of variation**	*d.f.*[a]	*MS*[b]	*F*[c]
Carapace	Island	2	0.11	73.060*
	CS	1	0.019	11.97*
	Island * CS	2	0.0036	2.29*
	Residuals	226	0.0016	
Abdomen	Island	2	0.072	93.89*
	CS	1	0.033	42.80*
	Island * CS	2	0.0022	2.95*
	Residuals	229	0.00076	
Chela	Chela	1	0.0019	0.44[ns]
	Island	2	0.13	29.36*
	CM	1	0.17	39.051*
	CS	1	0.38	87.28*
	Chela * CS	1	0.0022	0.50[ns]
	Island * CS	2	0.0057	1.30[ns]
	CM * CS	1	0.018	4.030*
	Chela * Island * CS	2	0.0044	1.0070[ns]
	Chela * CM * CS	2	0.010	2.29[ns]
	Chela * Island * CM * CS	2	0.0036	0.81[ns]
	Residuals	448	0.0044	

[a]*d.f.*, degrees of freedom. [b]*MS*, mean-squares. [c]*F*, *F*-value. *, significant p-value ($p < 0.05$). [ns], non-significant p-value ($p > 0.05$).

correlation for the abdomen ($r = 0.99$), and a strong negative correlation for the chelae ($r = -0.78$) (Fig. 5). Thus, complementing the morphometric-space results, which revealed high overlap among islands, each structure displayed a distinct trend of variation in relation to genetic distances.

DISCUSSION

We investigated the phenotypic variation in structured populations of the insular land crab *J. lagostoma* across three oceanic islands. Individuals displayed high variability within islands for all measured structures, particularly the chelae, confirming the presence of both chelar morphotypes in all populations. This is consistent with the maintenance of ancestral polymorphism or parallel adaptation in *J. lagostoma* populations, supporting our second hypothesis (H_2). Sexual dimorphism was the main driver of morphological variation, especially for abdomen and chelae growth, while subtle differences among islands were observed but were insufficient to indicate clear divergence. The strong overlap in both linear and geometric morphometric spaces suggests that stabilizing selection acts on these traits, consistent with our third hypothesis (H_3). Overall, these results indicate that despite genetic structuring among islands, adult males exhibit cryptic phenotypic divergence, and sex-stratified linear morphometrics reveal high intrasexual similarity.

It is noteworthy that the geometric morphometric analyses were restricted to males and therefore, all shape-based interpretations therefore refer exclusively to male morphology. Because due to time constraints in expeditions, we would not be able to take photographs of all males and females. Thus, our male-restricted analyses avoided potential confounding effects of sexual dimorphism on inter-island variation. We encourage future studies to include both males and females to further test whether similar interpretations occur in both sexes.

Land crab trait selection

Each structure analysed here has distinct biological functions associated with terrestrial adaptation or sexual dimorphism. Our results are consistent with the contrasting selective pressures acting on the carapace, chelae, and abdomen, but similarly across the Brazilian populations (Rocas Atoll, Fernando de Noronha, Trindade), suggesting similar selective patterns across islands.

The dimensions we measured in the carapace (or cephalothorax) are not only proxies for body size but can also be directly related to terrestrial adaptation. Land crabs have enlarged branchial chambers that favour the uptake of air humidity (Bliss and Mantel 1968, Britton *et al.* 1982, Vannini *et al.* 2003, Morris 2005, Lucu and Turner 2024). Consequently, their carapaces tend to be wider than longer (Hartnoll *et al.* 2006a, Lai *et al.* 2017), a pattern consistent across all islands in our study. Individuals from FN showed slightly wider carapaces, suggesting phenotypic plasticity to hotter, drier conditions, as FN often experiences a semi-arid climate (Rafael *et al.* 2021), unlike the other studied islands (RA and TR), which remain humid throughout the year (Teixeira 1996, Pedroso *et al.* 2018). Broader carapaces in gecarcinids provide enlarged branchial chambers, which improve moisture retention and reduce desiccation risk. This subtle difference observed in FN may reflect plastic or adaptive adjustments to local microclimatic constraints. Future experimental approaches could test whether these differences represent local adaptation.

Conversely, both the abdomen and chelipeds act as secondary sexual traits in crabs (Hartnoll 1974, McLay and Becker 2015). Among them, abdomen width was the main variable distinguishing the sexes, reflecting its functional role: in females, broader abdomens enhance brood protection and reproductive success; in males, it mainly protects the copulatory appendages (Baeza and Fernández 2002, González-Pisani *et al.* 2017). The low variability and strong similarity among islands suggest a stable selective regime for this structure.

Chelipeds, in turn, showed the highest variability among traits. Although sexual dimorphism is present, it is not strongly marked. Even though chelipeds are used by males in visual displays during courtship (Hartnoll *et al.* 2006b, João *et al.* 2021), in both sexes their continuous growth throughout ontogeny may reflect multiple functions (Mariappan *et al.* 2000). For example, the use of chelipeds as weapons is widespread in crabs to defend against predators (Claussen *et al.* 2008), such that larger chelae provide a greater chance of winning than overall body size (Yoshino *et al.* 2011). However, this is less associated with the life history of *J. lagostoma*, as no specific predators are found on these islands (João *et al.* 2023). Still in the context of fighting, male individuals

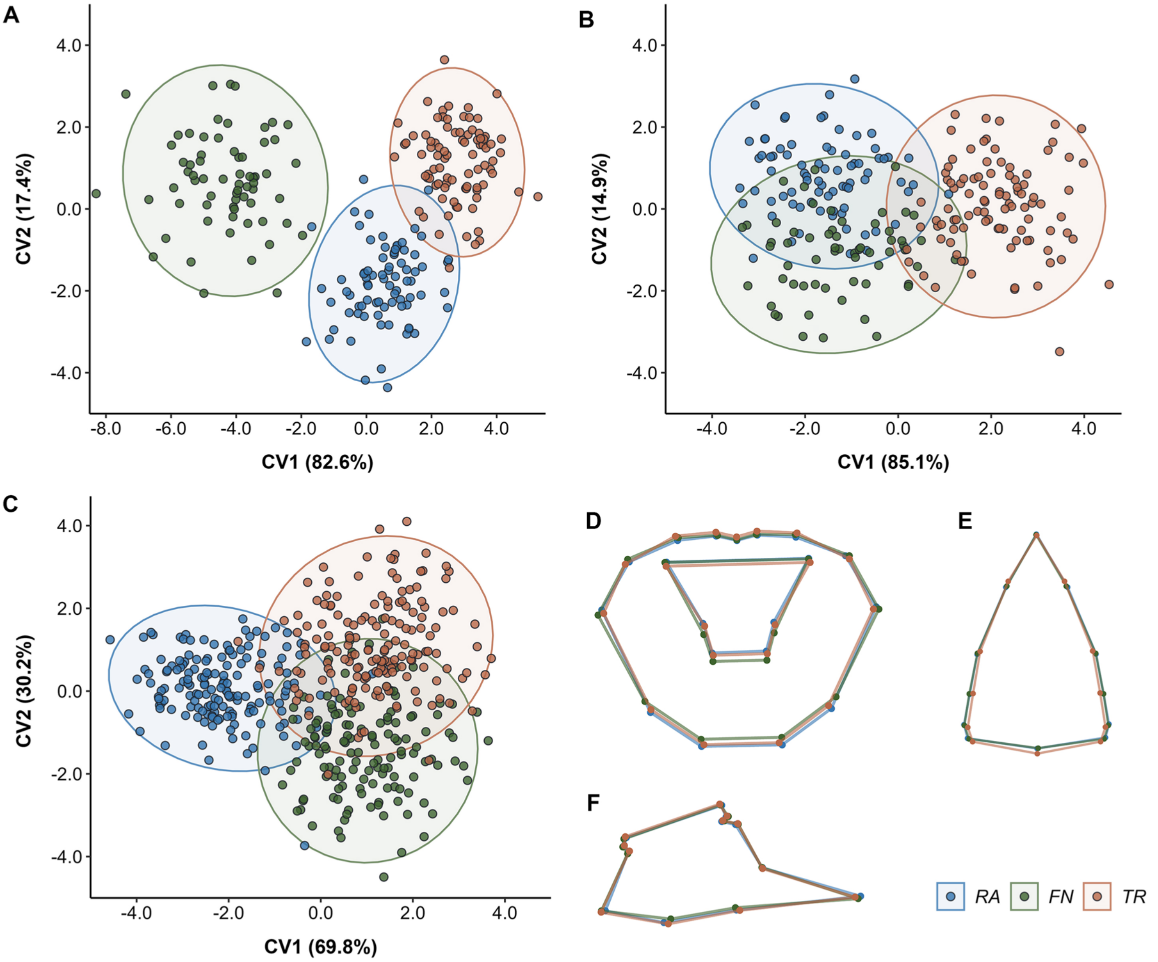

Figure 4. Geometric morphometric variation of *Johngarthia lagostoma* among the three oceanic islands (RA, Rocas Atoll; FN, Fernando de Noronha; TR, Trindade Island). A–C, Canonical Variates Analyses (CVA) of the carapace (A), abdomen (B), and chelae (C). D–F, Mean shape configurations for the carapace (D), abdomen (E), and chelae (F) on each island.

Table 4. Matrix of morphometric (A–C) and genetic (D) distances calculated for *Johngarthia lagostoma* based on pairwise comparisons among the three oceanic islands (RA, Rocas Atoll; FN, Fernando de Noronha; TR, Trindade Island). In A–C, the lower and upper diagonals correspond to Euclidean and Mahalanobis distances, respectively, calculated for the carapace, abdomen, and chelae. In D, the lower and upper diagonals correspond to F_{ST} and Φ_{ST}, respectively, both reported by Rodríguez-Rey *et al.* (2016)

A	Carapace	RA	FN	TR	B	Abdomen	RA	FN	TR
	RA	–	0.049	0.022		RA	–	0.022	0.017
	FN	2.20	–	0.071		FN	1.55	–	0.0053
	TR	1.93	2.34	–		TR	1.92	1.92	–
C	**Cheliped**	**RA**	**FN**	**TR**	**D**	**Genetic**	**RA**	**FN**	**TR**
	RA	–	0.71	0.74		RA	–	0.00	0.44
	FN	2.01	–	0.023		FN	0.00	–	0.50
	TR	1.95	1.77	–		TR	0.19	0.28	–

of several animal taxa evolved disproportionately larger weapons for male-male combat as a consequence of intrasexual selection (Anderson 1994, Emlen 2008, Yoshino *et al.* 2011). Because fights between *J. lagostoma* males are rare, at least during copulatory behaviour (João *et al.* 2021), we argue that selective pressure favouring weapons for combat is unlikely. Also, cheliped growth and shape are often linked to feeding strategies or correlated with preferential food items (Spani *et al.* 2020). Given that *J. lagostoma* is an opportunistic species feeding on plant material, carrion, and vertebrate juveniles (Teixeira 1996, Andrades *et al.* 2019, Tavares and Mendona 2022, Kriegler 2024), the observed morphological variability may reflect a broad trophic repertoire rather than sexual selection or combat.

Chelar polymorphism was consistently observed across islands, with both homochelous and heterochelous individuals occurring in roughly balanced proportions. This pattern, also reported for

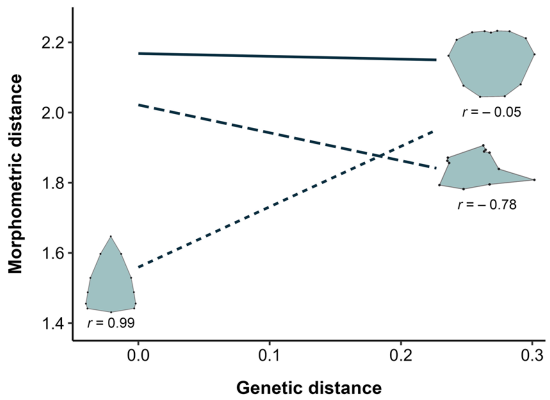

Figure 5. Association between morphometric (Mahalanobis) and genetic distances (FST, reported for Rodríguez-Rey *et al.* 2016), estimated by pairwise comparisons for each structure (carapace, abdomen, and chelae) among the three oceanic islands (RA, Rocas Atoll; FN, Fernando de Noronha; TR, Trindade Island) for *Johngarthia lagostoma*.

Ascension Island (Hartnoll *et al.* 2017), has been rarely documented among crabs (João *et al.* 2024b). Generally, species exhibit heterochely in almost all adult males, likely as an outcome of sexual selection (Crane 1975, Rosenberg 2001). Since both morphs have access to receptive females and no evidence supports distinct functional roles between the morphotypes of the chelae (crusher: with more robust teeth; and cutter: with comparatively sharper and finer teeth), the persistence of this polymorphism may simply reflect neutral variation or individual specialization (Garner and Neff 2020). However, the lack of integrated shape–function studies for this species limits further interpretation (Palaoro and Peixoto 2022). So, the combination of balanced morphotype frequencies and the absence of evidence for distinct functional roles between morphs suggests that ancestral cheliped polymorphism has been retained rather than replaced by directional selection for a single configuration. Similar persistence has been reported in other decapods inhabiting environments with low predation pressure and limited male–male combat (Hartnoll *et al.* 2017, Palaoro and Peixoto 2022), indicating that weak directional selection and functional redundancy may underlie this tendency. So, we suggest that the maintenance of both homochelous and heterochelous forms in *J. lagostoma* is not exceptional, but rather the relatively stable ecological conditions favour the long-term retention of cheliped polymorphism.

Interestingly, when we associate genetic and morphometric distances among islands, a contrasting pattern emerged across the evaluated traits. The male abdomen, arguably the only functionally neutral character in our study, showed a positive association with genetic divergence. In contrast, the carapace and chelae, which have recognized ecological and reproductive roles, displayed no association and a negative relationship, respectively. This mismatch suggests that the phenotypic variation is primarily shaped by selective pressures acting on each trait, overriding the expected genotype–phenotype correspondence. Such a decoupling between genetic and phenotypic divergence is not surprising and was previously documented (Kozak *et al.* 2011). Because only three inter-island comparisons are available, these phenotype–genotype relationships must be interpreted strictly as descriptive trends rather than inferential evidence.

Evolutionary mechanisms underlying phenotypic similarity

The comparisons between previously identified genetic groups of *J. lagostoma* (AR + FN and TR) revealed a consistent pattern of phenotypic similarity. Both linear and geometric morphometric analyses showed strong overlap among islands, and chelar polymorphism occurred in close frequencies regardless the population from which crabs were sampled. Thus, regardless of the selective regime acting on each trait, *J. lagostoma* populations exhibit highly similar phenotypes. These results are consistent with the maintenance of ancestral polymorphism (H_2) and stabilizing selection acting on subtle or cryptic phenotypic variation (H_3) (Fig. 6).

Among studied structures, only the carapace showed slight, non-significant variation among islands, whereas the remaining traits displayed extensive overlap. This contrasts with the broader macroecological trend in which island populations typically show greater phenotypic divergence than mainland systems (Csergő *et al.* 2024). Therefore, our findings allow us to reject divergent selection or genotype–phenotype structuring across islands as underlying evolutionary mechanism shaping these *J. lagostoma* traits. This reinforces the notion that lineage isolation alone does not necessarily lead to phenotypic divergence (Lande 1980, Zamudio *et al.* 2016). It also aligns with the geological context of the three islands—the Rocas Atoll rests on biogenic substrate dated to ~6 kya (Kikuchi and Leão 1997); Fernando de Noronha rests on volcanic substrates dated to ~12.5 Mya, exhibiting a younger eruptive phase in the Early Pleistocene (Hachich *et al.* 2015); and Trindade origin dated to ~3.7 Mya in the middle Plio-Pleistocene (Freire *et al.* 2021)—which suggests that their relatively recent origin and long-term environmental stability may limit morphological differentiation (Stayton 2015).

The evolutionary history of *J. lagostoma* is relatively recent, mirroring that of the South Atlantic oceanic islands, which are geologically young (Hachich *et al.* 2015). Although the Gecarcinidae family originated ~50 Mya (Tsang *et al.* 2022), the colonization of insular terrestrial habitats by *Johngarthia* species likely occurred within the last 10 Mya (Tsang *et al.* 2014, 2022, Guinot *et al.* 2018). Thus, both the islands and *J. lagostoma* lineages originated during the Miocene, when terrestrial diversification of several taxa intensified (Steinthorsdottir *et al.* 2021). We speculate that, because the ancestor of *J. lagostoma* was likely already adapted to terrestrial environments, current populations, such as those we studied, probably retained ancestral phenotypes rather than evolving through recent convergence. This relatively short evolutionary timescale may have led to limited opportunities for phenotypic divergence among islands.

In addition to historical factors, the environmental context of terrestrial habitats in these islands likely contributes to the phenotypic stability of *J. lagostoma*. Despite physical isolation, oceanic islands generally present a long-term environmental stability (Escobar-Camacho *et al.* 2021), and the Brazilian islands share several similar environmental conditions (Pinheiro *et al.* 2018). Therefore, *J. lagostoma* populations experience similar ecological conditions in terrestrial environment across these islands, including vegetation cover, food availability, and absence of predators or interspecific competitors. This pattern contrasts with that observed in other species that co-occur on the same islands, such as *Grapsus grapsus*, a semi-terrestrial crab that inhabits the supratidal splash zone of rocky shores. In this species, differences in carapace and

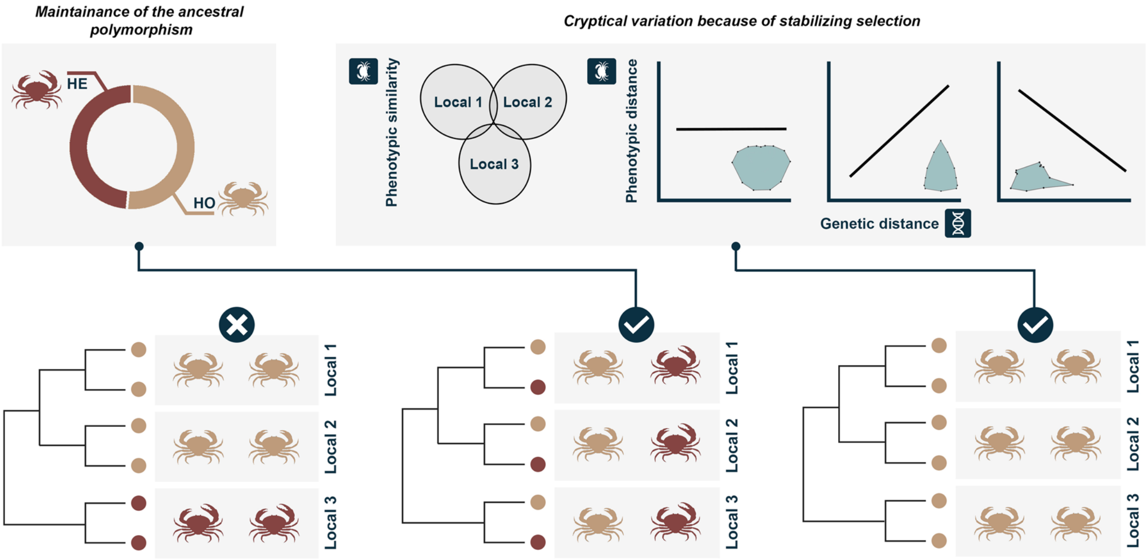

Figure 6. Conceptual representation of phenotypic variation in *Johngarthia lagostoma* among geographic locations and/or populations, highlighting the three evolutionary scenarios: H1, phenotypic divergence (left); H2, retention of ancestral polymorphism (centre); and H3, cryptic or undetectable phenotypic variation maintained by stabilizing selection (right). Distinct colours of crab icons represent the possible phenotypic outcomes under each evolutionary scenario. Local 1, Local 2, and Local 3 represent Rocas Atoll, Fernando de Noronha, and Trindade, respectively. These islands are in the specific context of the recent origin (6 kya for Rocas Atoll, 12.5 Mya for Fernando de Noronha, and 3.5 Mya for Trindade) and the restricted larval connectivity imposed by distance and oceanic currents.

chelae shape between islands have been reported and interpreted as the result of habitat-specific selective pressures to contrasting environments and community composition affecting carapace morphology, as well as differences in food availability influencing chelae shape (Teschima *et al.* 2016). Arguably, this represents a more heterogeneous and less stable environmental scenario than that experienced by *J. lagostoma*, suggesting that its terrestrial lifestyle may contribute to the phenotypic similarity we observed.

Analogous environmental conditions across islands presumably result in similar selective pressures acting on each population (Barrett and Schluter 2008). Such conditions may promote the maintenance of ancestral genetic variation, leading to recurrent expression of similar phenotypes even in disconnected lineages (Stern 2013). Accordingly, the widespread occurrence of chelar polymorphism in *J. lagostoma* supports both the retention of ancestral variation and the possibility of parallel evolution. Shared discrete phenotypic variation among genetically structured populations has been reported in several taxonomic groups (Colosimo *et al.* 2005, Tishkoff *et al.* 2007, Pearse *et al.* 2014, Pfenninger *et al.* 2015). Several mechanisms could explain the persistence of polymorphism within and between populations, including balancing selection and independent adaptive responses to similar ecological settings (Magalhaes *et al.* 2015, Cerca 2023). Moreover, when the relative frequencies of morphs are balanced—as observed in our data—the likelihood of long-term maintenance increases (Jamie and Meier 2020).

The high phenotypic similarity among all analysed traits further aligns with the environmental similarity previously reported for these oceanic islands. Such patterns of genetically structured populations with cryptic phenotypic variation are expected when strong barriers restrict gene flow, generating genetic divergence, while comparable selective environments persist across space and time (Zamudio *et al.* 2016). Nonetheless, the morphometric traits analysed here are likely under selective pressures in all populations, and thus, their similarity cannot be directly attributed to the absence of selection. We can also observe this by the lack of association between genetic and morphometric distances in the most functionally relevant traits. This pattern, together with the high similarity, supports the hypothesis of cross-island stabilizing selection. This evolutionary mechanism acts by maintaining optimal traits (Hansen 1997) and could explain morphological similarity among disconnected populations, as reported for several taxa (Schubart *et al.* 2001, Paupério *et al.* 2012, Barley *et al.* 2015, Reilly and Wake 2015). This is particularly evident for traits associated with ecological performance, niche occupation, and sexual selection (Hunt *et al.* 2009, Punzalan and Rowe 2016), such as the structure analysed here.

Our findings highlight the value of endemic oceanic island species as models for understanding evolutionary mechanisms. Further exploration of genetic diversity associated with phenotype in insular organisms will be essential for addressing future challenges under changing environmental conditions. Large and genetically diverse populations are more likely to retain alleles that allow adaptive response to environmental shifts, helping maintain stable phenotypes (Bell 2013). In insular environments, however, increasing threats from climate change and biological invasions (Taylor and Kumar 2016, Veitch *et al.* 2019) may alter selective regimes and, consequently, the phenotype of endemic species. Therefore, efforts to establish genotype–phenotype associations in invertebrates should be strengthened, as these studies remain far less common than those conducted in vertebrate taxa (Zamudio *et al.* 2016).

CONCLUSION

Our study provides an integrative comparison of phenotypic variation in *J. lagostoma* across three South Atlantic oceanic islands. Despite the genetic structuring and isolation among populations, we observed a phenotypic similarity, with overlap in both linear and geometric morphometric spaces. In addition, the expression of chelar polymorphism was consistent across all islands where *J. lagostoma* occurs.

The mismatch between genetic and phenotypic distances, together with the high phenotypic similarity, suggests that morphological traits in this species are shaped primarily by stabilizing selection and the retention of ancestral polymorphism. The geological youth, environmental stability, and low predation pressure across the oceanic islands likely contribute to the persistence of similar phenotypes. These shared phenotypic trends across populations also has conservation implications, as it raises questions about the resilience or vulnerability of *J. lagostoma* to future environmental change.

Finally, by documenting patterns of morphometric variation, our findings highlight *J. lagostoma* as a valuable model for studying evolutionary processes in insular terrestrial ecosystems. Ongoing shifts in island environments, including climate change and biological invasion, may rapidly alter selective regimes and influence phenotypic trajectories of endemic species. Continued monitoring will therefore be essential to detect potential changes in selection and to understand whether and how phenotypic variation responds over time.

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AUTHOR CONTRIBUTIONS

Conceptualization, discussions, writing, review, and editing: M.C.A.J., G.M.M., and M.A.A.P.; methodology, formal analysis, and original draft preparation: M.C.A.J.; project administration: M.C.A.J. and M.A.A.P.; supervision: G.M.M. and M.A.A.P. All authors have read and agreed to the final version of the manuscript.

SUPPORTING INFORMATION

Supplementary data is available at *Biological Journal of the Linnean Society* online.

CONFLICT OF INTEREST

The authors declare no competing interests.

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DATA AVAILABILITY

The data and R scripts are available in the authors' GitHub repository https://github.com/marcio-joao/john_morph_comparison.

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