Research article

Insular dwarfism in *Akymnopellis chilensis* (Gervais, 1847) centipedes from the Humboldt Archipelago, Chile
(Chilopoda: Scolopendromorpha, Scolopendridae)

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Abstract
Body size is a key morphological trait that reflects both the evolutionary history and ecological processes of species and is commonly used in assessing biogeographic patterns. Foster's rule predicts changes in body size associated with insularity, often manifested as dwarfism or gigantism. In this study, we tested this rule in *Akymnopellis chilensis* (Gervais, 1847) (Chilopoda, Scolopendromorpha), using specimens from the Humboldt Archipelago (Chile) and the mainland. Robust statistical analyses and generalized linear models reveal that insular individuals exhibit significantly reduced body sizes relative to mainland populations. Furthermore, mean annual temperature emerged as a key predictor of body size variation. This study provides the first documented evidence of insular dwarfism in myriapods, extending the applicability of Foster's rule to a previously underrepresented group of terrestrial arthropods. Our findings underscore the importance of insularity and climate change as selective pressures influencing the morphological evolution of invertebrates, with implications for the conservation of endemic taxa in fragile island ecosystems.

Keywords: insularity, Foster's rule, body size evolution, Scolopendromorpha, centipedes, climate change.

Introduction

Body size is a widely used morphometric measure to explain biogeographic rules, as it is closely related to the physiology and evolutionary history of organisms (Lokatis & Jeschke 2018; Cornejo et al. 2022). Thus, current body size is considered the result of both historical and ecological processes. In this context, geographically isolated animal populations have long served as key study models to explain body size evolution. Biogeographic hypotheses such as Foster's Rule have emerged from scientific records showing that island populations often exhibit smaller body sizes than their continental counterparts. That is, larger animals tend to become smaller—an attribute recorded across a wide range of tax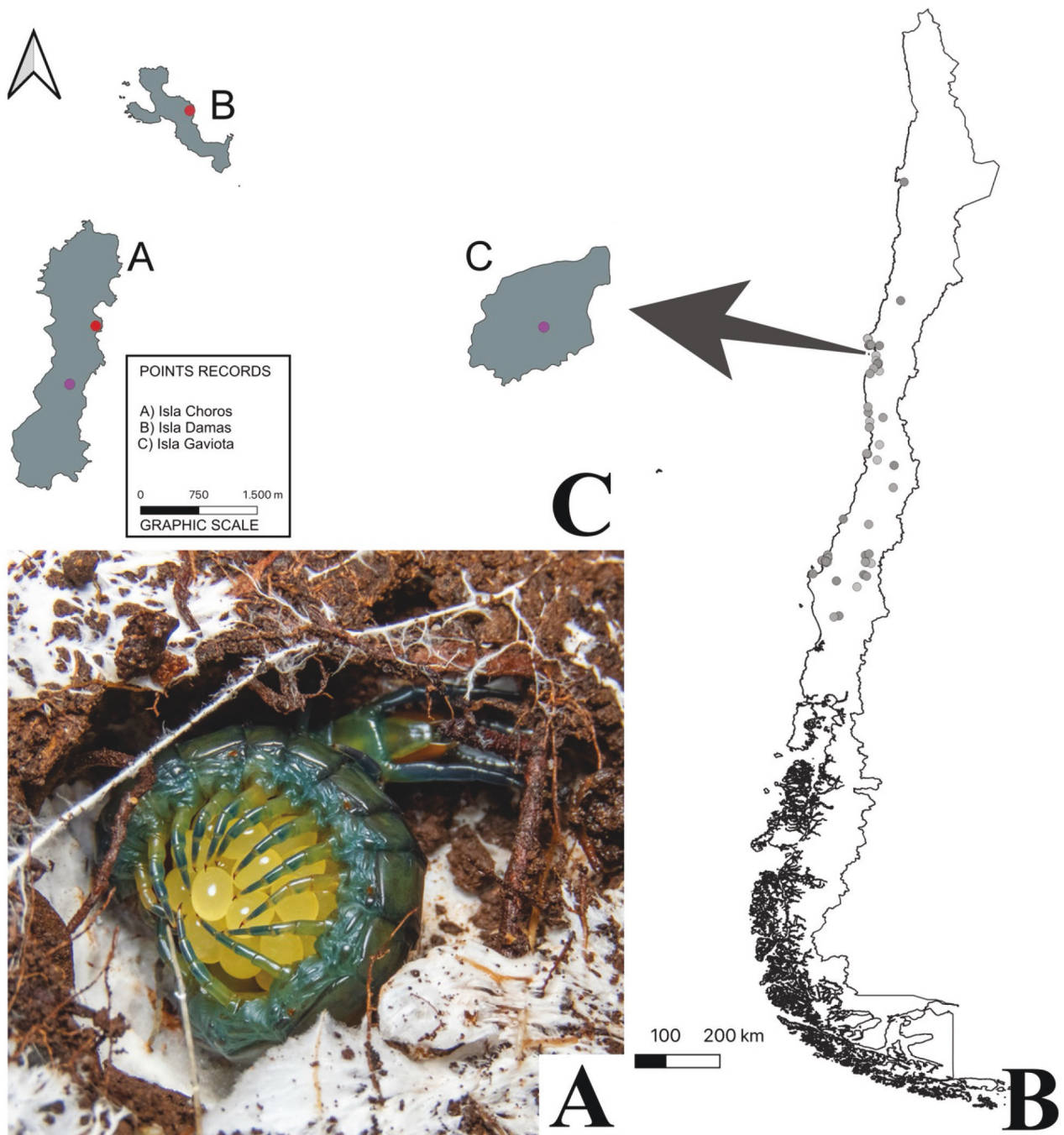a including mammals, snakes, fish, mollusks, reptiles, and even insects (Brown & Maurer 1989; Brown et al. 1993; Blackburn & Gaston 1994; Maurer 1998; Keogh et al. 2005; Meiri 2008; Cornejo et al. 2022).

Foster's Rule, also known as the Island Rule, refers to cases of gigantism or dwarfism in insular species (Cornejo et al. 2022). Foster (1964) demonstrated body size variation in island mammal species, confirming that in some carnivores, Lagomorpha, and Artiodactyla, insular individuals were smaller than their continental counterparts. Unlike other biogeographic rules, Foster's Rule lacks a clearly defined causal mechanism explaining the phenomenon. It is believed that for species with large body sizes, islands often pose a challenge due to limited food resources per unit area. Consequently, these species tend to reduce their body size to the point where the available resources are sufficient to meet

the energetic demands of individuals over time (Cornejo et al. 2022). In contrast, smaller-bodied species often find new opportunities on islands, benefiting from the absence of negative biological interactions such as predators, limited resource access, reduced competition, and even the occupation of vacant ecological niches (Cornejo et al. 2022).

In Chile, the order Scolopendromorpha is represented by the families Cryptopidae and Scolopendridae. The latter includes the genus *Akymnopellis* Shelley, 2008, which shows a wide distribution (three species are known from Chile) with records across various environmental gradients throughout the country, including some northern and southern islands (Shelley 2008; Vega-Román & Ruiz 2018). *A. chilensis* (Gervais, 1847) exhibits unique morphological and physiological traits that may reflect adaptation to its environment, such as body length—a key trait in thermoregulation. For these reasons, the objective of this study was to evaluate the presence of the Island Rule (Foster's Rule)

Fig. 1 – A, Female *Akymnopellis chilensis* (Gervais, 1847) guarding her eggs (photograph by Claudia Maureira); **B**, Points record from Continental Chile; **C**, Points record from Island Chile.

Table 1 – Coefficients of the generalized linear models (GLMs) for body size.

Models	AIC	Intercepto	Devianza (%)	F-value	P-value
Mod 1. TMEAN	1575	41	16.54	3.173	0,0003
Mod 2. COL FECH	1578	1578	16.78	2.736	0,0010
Mod 3. ADIT.	1586	1586	22.98	1.195	0,289
Mod 4. INTER.	1589	1589	33.20	0.460	0,709

in *A. chilensis*. It is hypothesized that insular specimens will exhibit smaller body sizes due to limiting conditions on the islands of the Humboldt Archipelago, compared to their continental congeners, thereby demonstrating a case of insular dwarfism.

Materials and Methods

A total of 206 specimens of *Akymnopellis chilensis* were included in this study. 69 specimens were collected on islands and 137 on the continent. Specimens were collected from the islands of the Punta de Choros Archipelago (Isla Damas, Isla Choros, and Isla Gaviota), as well as from various locations along continental Chile. Collections were carried out using active searching and pitfall traps between the years 2006 and 2024 (Fig. 1A, B, C). The specimens are deposited in the arthropod collection of the Ecological Entomology Laboratory, University of La Serena, Chile (LEULS).

Each specimen was measured for total body length, from the cephalic plate to tergite 21 (sensu Shelley 2008). For specimens preserved in alcohol, the length of each tergite was measured individually, and the sum of these lengths was considered as the total body length (Shelley 2008). Each individual specimen was observed by stereoscopic microscopy and its taxonomic characteristics were analyzed using specific classification keys based on characters of taxonomic importance such as cephalic plate, cervical groove, coxosternite, among others (Shelley 2008).

To assess differences in body size between insular and continental specimens, the means were compared using Yuen's trimmed mean test (Yuen 1974), applying a 20% trimming level**.** Unlike other statistical tests, Yuen's test is not sensitive to the assumption of homogeneity of variance, thus reducing Type I error rates when the dataset does not meet this assumption (Ramalle-Gómara & de Llano 2003).

To detect temporal changes in body size, four generalized linear models (GLMs) were evaluated. Since many of the specimens were at juvenile stages or their preservation status made accurate sex determination difficult, this variable was excluded to avoid introducing biases associated with incomplete or unreliable classification. The predictor variables included collection year (COLFECH) and the mean temperature (TMEAN) of each locality.

Data were obtained from https://explorador.cr2.cl, which provides updated information for each locality. The first model assessed the relationship between body size and TMEAN only; the second model evaluated the relationship between body size and collection year (COLFECH); the third model included an additive effect of both variables (TMEAN + COLFECH). The variables mean annual temperature (TMEAN) and collection year (COLFECH) were selected due to their direct relevance to the physiology of ectothermic organisms such as myriapods. Ambient temperature affects key processes such as growth, metabolic rate, and thermoregulation, and it is one of the most commonly used factors to explain patterns of morphological variation under climate change scenarios (Entling et al. 2010; Yom-Tov & Geffen 2011).

We prioritized climatic and temporal predictors (TMEAN, COLFECH) due to their direct physiological relevance for ectotherms and their consistent spatiotemporal coverage. Additional ecological variables (habitat structure, resource availability, biotic interactions) were considered; however, limitations in resolution and comparability led us to exclude them to prevent overfitting and collinearity. Sensitivity analyses (Appendix S1) indicate that our conclusions regarding insular dwarfism and the effect of TMEAN are robust to alternative specifications and environmental proxies.

Collection year allows for the evaluation of temporal changes associated with global warming and serves as a useful proxy variable to capture potential evolutionary trends or plastic responses accumulated over time. And the fourth model tested an interaction effect between them. Finally, the significance of model coefficients was assessed using an analysis of variance (ANOVA) (Zuur et al. 2007; Cornejo et al. 2022).

The analyses were carried out in the statistical program R 4.0.2.

Results

The *Akymnopellis chilensis* specimens collected on the mainland had an average body length of 39.54 mm**,** while those from the islands had an average of 33.36 mm**.** According to Yuen's trimmed mean test (T = 5.984; p = 9.65 × 10^{-8}), island specimens are significantly smaller than those from the mainland (Fig. 2).
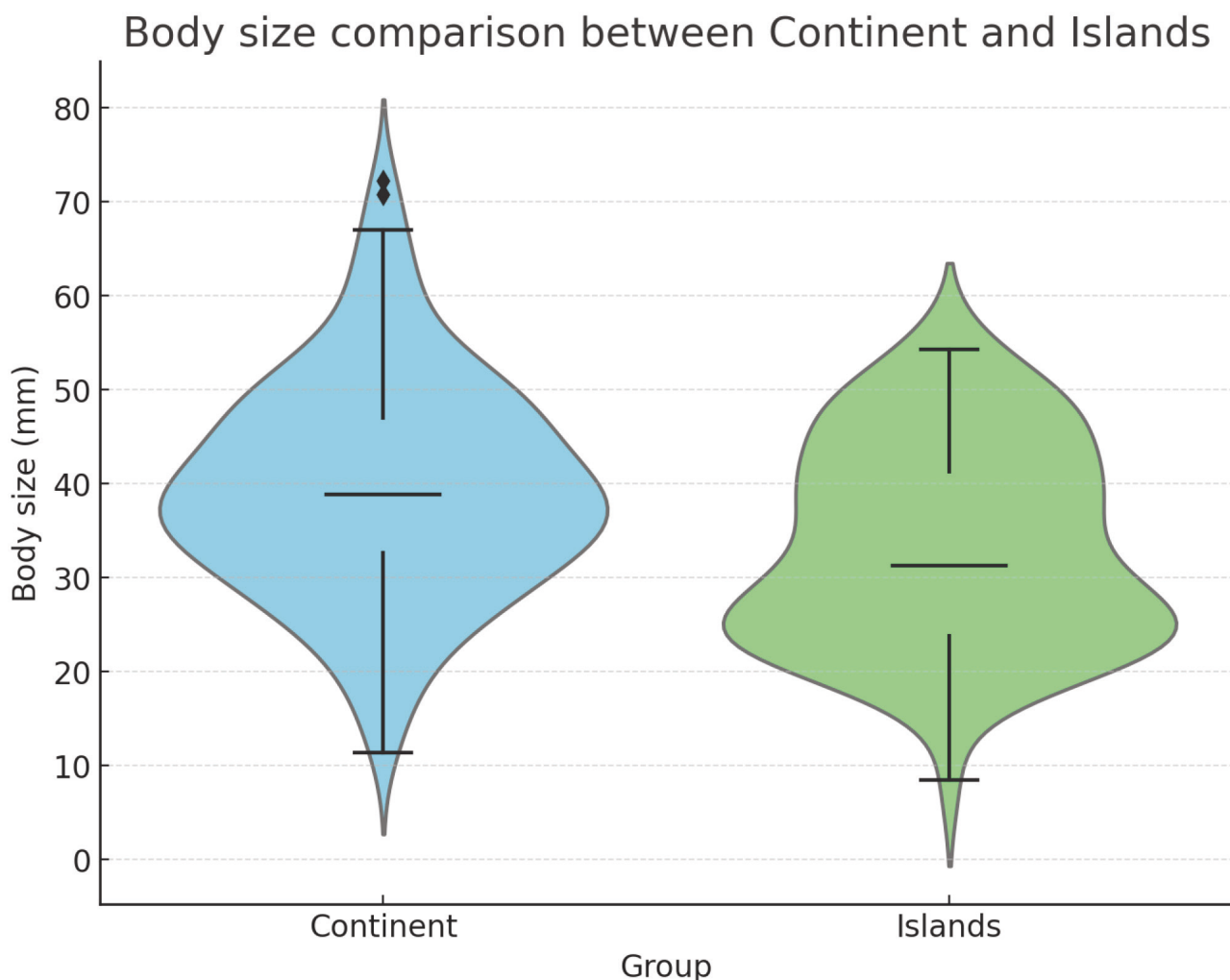
The best-fitting GLM corresponds to model 1: TMEAN (AIC = 1575). The AIC, or Akaike Information Criterion (AIC), is a statistical measure that evaluates model quality by balancing goodness of fit with model complexity; lower values indicate a better and more parsimonious model. Although model 4 presents a significant interaction between TMEAN and COLFECH, it has the highest AIC and is therefore the least parsimonious. Model 3 does not include any significant predictors and has a high AIC, indicating that adding predictors does not improve model fit. Finally, model 2, which includes only the collection year (COLFECH) as a predictor, is statistically significant but accounts for less variability than model 1 (TMEAN) (Table 1).

Additionally, when analyzing deviance explained by each model, results show that model 4 (INTER) accounts for approximately 33.20% of the variability, indicating greater predictive power. This suggests that the interaction between mean temperature and collection year (COLFECH) is relevant for understanding body size variation.

Discussion

The results support the idea of dwarfism in *Akymnopellis chilensis*, as insular specimens were significantly smaller than those collected on the mainland (Fig. 2). This constitutes the first recorded instance of this phenomenon in myriapods, opening a new line of research to explore the biological processes underlying this biogeographic pattern. Entling et al. (2010) identified a clear relationship between body size and climate (temperature) in European spiders, showing that average body size increased from cold and humid environments to warm and dry ones.

Moya-Solà & Köhler (2003) studied the evolution of *Oreopithecus bambolii* Gervais, 1872, (Primates, Dendropithecidae) demonstrating that a finite geographical area, trophic resource limitation, and the absence of terrestrial predators were the main ecological factors acting as selective pressures. However, there are several unconsidered variables that could help explain why miniaturization occurs in insular

Fig. 2 – Average body size of *A. chilensis* (Gervais, 1847). Violin plot showing the full distribution of body sizes in each group (continent and islands), overlaid with a boxplot to highlight medians and interquartile ranges.

specimens. It is likely that in island habitats, intraspecific or interspecific competition may favor the selection of smaller individuals. In the absence of predators, arthropods may evolve toward smaller sizes in order to more efficiently exploit habitat space and improve the allocation of resources.

Another important point is that our results confirm mean annual temperature (TMEAN) as a key factor influencing body size in these arthropods, and that this effect is also associated with collection year (COLFECH). These findings are consistent with previous studies that link body size variation in ectotherms to temporal and thermal conditions (Reading 2007; Yom-Tov & Geffen 2011; Garden et al. 2009; Messmer et al. 2017; Fajardo et al. 2019; Mundiger et al. 2022). Although our analyses did not directly evaluate global warming, the association between body size and temperature supports the view that ongoing climatic changes may indirectly influence morphological traits. This study also provides valuable data for understanding how insular habitat characteristics influence the evolution and ecology of terrestrial organisms and highlights how environmental conditions in the Punta de Choros Archipelago (e.g., limited resources, competition, predation pressure) may shape the morphology of myriapods compared to their mainland counterparts.

Another relevant aspect is that our findings support the idea that mean annual temperature influences body size in arthropods, particularly ectotherms whose physiology depends directly on environmental conditions (Ohlberger 2013). One of the most recurrent responses described in the literature is a reduction in body size, which can be explained by phenotypic plasticity—i.e., reversible developmental changes in response to temperature variation (Entling et al. 2010). Such plasticity allows individuals to rapidly adjust to warmer environments, optimizing metabolic efficiency and resource use. Over longer timescales, these conditions may also act as selective pressures favoring genotypes associated with smaller body sizes, thereby initiating microevolutionary processes (Mundiger et al. 2022). Distinguishing between plastic and evolutionary responses is therefore essential for understanding the adaptive mechanisms of arthropods in the face of ongoing climatic changes (Yom-Tov & Geffen 2011).

Although our models focused on climatic and temporal predictors, future research should integrate ecological variables such as habitat structure, resource availability, and interspecific interactions, in order to provide a more comprehensive understanding of the mechanisms driving body size variation in insular centipede populations. The confirmation of insular dwarfism in *A. chilensis* highlights the vulnerability of island populations to ecological perturbations, reinforcing the need for conservation strategies tailored to fragile insular ecosystems.

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