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Original Article

Microgeographic diversity does not drive macroevolutionary divergence in bite force of the Ibiza wall lizard, *Podarcis pityusensis*

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Abstract

Despite extensive research, it is still poorly understood how microgeographic phenotypic variation translates to the macroevolutionary level. Here, we use the Ibiza wall lizard, *Podarcis pityusensis*, an endemic species of the Balearic Islands, to study microgeographic variation across different scales of evolutionary isolation. We quantify bite force and morphology alongside biotic and abiotic environment in 11 populations, which have been variably isolated from one another over the Quaternary period. While we generally find increasing divergence in form and function as populations become more isolated from each other, this is not true when isolation is the highest; phenotypic differences between the 2 major clades of *P. pityusensis* are negligible, despite populations being isolated for over 100,000 years. Our results show that how environmental selective pressures drive form–function evolution differ by sex. Natural selection appears the most important driver of female evolution, while male phenotypes are apparently driven by both natural and sexual selection, but precise drivers of form–function evolution vary according to the scale of isolation investigated. Our study demonstrates incongruence in form–function–environment relationships within a constrained geographical area, highlighting how convergence at greater evolutionary scales can obscure microevolutionary diversity.

Keywords: bite force, environmental drivers, evolutionary scales, sexual dimorphism, Lacertidae, Balearic Islands

Introduction

Adaptation of populations to their surroundings generates genomic and phenotypic diversity, which act as the building blocks of speciation, cumulating to form large-scale macroevolutionary changes observable in the fossil record (Arnold et al., 2001; Dietrich, 2009; Gould, 1994; Hendry & Kinnison, 2001; Li et al., 2018). Therefore, to elucidate the true diversity of life on Earth, it is important to understand how adaptation translates across scales, from populations up to the species level and beyond. This topic, known as "evolutionary scaling," has witnessed significant empirical and theoretical advances in recent years, yet whether evolutionary trajectories scale consistently across taxonomic ranks or geological timescales remains controversial (see Rolland et al., 2023; Schluter, 2024; Tsuboi et al., 2024, and references therein). Studying the smallest scale of evolution, i.e., adaptations of individuals within a population, is hugely powerful in this context (Simon et al., 2025; Taverne et al., 2021), as it confers opportunities to investigate how environmental selective pressures drive different selective regimes, which may lead to diverging phenotype, as is often observed between males and females (Dawson & Geber, 1999; Herrel et al., 1996, 1999; Shine, 1989). Investigating whether patterns of sexual dimorphism at the population level can be scaled up to the species or genus level is highly valuable for our understanding of how environmental selective pressures drive natural and sexual selection across micro- and macroevolutionary scales.

Bite force is a useful trait through which to study sexual dimorphism within the context of form–function–environment questions due to the roles biting serves in feeding, predator defense, and intraspecific combat (see Anderson et al., 2008, and references therein). These multiple roles mean that bite force can be used as a proxy for fitness, with direct links between bite performance and reproductive success (e.g., Lappin & Husak, 2005). Eco-evolutionary dynamics of bite force have been studied extensively in reptiles; in most species males bite more strongly than females (Herrel et al., 1996, 2007; Li et al., 2023), but in some taxa, such as chameleons (Silva et al., 2014) and turtles (Herrel et al., 2018), females bite more strongly than males. Herrel et al. (1996) suggest that in groups where males bite more strongly than females, sexual dimorphism may be driven by either natural selection, i.e., by niche divergence, or sexual selection, either male–male combat for mates or intersexual combat during mating, i.e., copulatory bites. There may also be an interplay between both factors (see Gvozdík & Van Damme, 2003; Herrel et al., 1996, 1999, and references therein). Studying the evolution of bite force within populations is therefore an excellent way to shed light on

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microevolutionary selective drivers at the smallest of scales, which can be directly translated and tested on larger evolutionary scales.

Over the last two decades, *Podarcis* lizards, endemic to the Mediterranean Basin (Arnold, 1973; Arnold & Burton, 1978), have become a model taxon for studies on rapid evolution of functional morphology, the findings of which have relevance to concepts of evolutionary scaling. Fascinating insights have come from *Podarcis* studies investigating the interplay of sexual and natural selection on the macro- (Kaliontzopoulou et al., 2012) and micro-evolutionary scales (Brecko et al., 2008; Donihue et al., 2023; Gomes et al., 2018; Patti et al., 2023; Runemark et al., 2015), as well as linking the two (Taverne et al., 2020, 2021, 2023). In this study, we focus on a particularly diverse species, the Ibiza wall lizard, *Podarcis pityusensis* (Boscá, 1883). Twenty-three currently recognized *P. pityusensis* subspecies are endemic to the Pityusic Islands, including Eivissa, Formentera, and 42 islets in the Balearic Islands in the Western Mediterranean (Pérez-Mellado, 2009; Salvador, 1984). This species shows huge diversity in phenotype (size, body proportions, and coloration) and life history (habitat, diet, and population densities) (Pérez-Mellado, 2009), yet remarkably low genetic diversity, classified as a single species with two major clades, one originating in Ibiza and one in Formentera (Rodríguez et al., 2013). In this study, we analyze bite force, body size, and head morphology of 11 populations of *P. pityusensis*, comprising seven islet and four main island (three from Ibiza and one from Formentera) sites. The sites included vary markedly in food resources, physical geography, intraspecific competition, and predator abundance, which we have quantified at each location, enabling us to perform a highly comprehensive evaluation of how different environmental selective pressures impact form and function in this species.

Our work will operate under a series of hypotheses aiming to investigate evolution of form–function–environment relationships across scales of evolutionary separation.

Hypothesis 1 investigates the morphological underpinnings of bite force. We hypothesize that there will be sexual dimorphism; that males have a larger body size and head than females, and further, that this morphological sexual dimorphism will underpin a higher bite force in male *P. pityusensis* than females, as observed in other *Podarcis* species (Brecko et al., 2008; Gomes et al., 2018; Kaliontzopoulou et al., 2012; Patti et al., 2023; Verwaijen et al., 2002).

For hypothesis 2, we assess evolutionary scaling of form–function relationships. We test this by creating five levels of increasing isolation: within 0.1 km, within 1 km, across islets, across a single clade, and between major clades. We predict that phenotypic differences will accumulate in populations via adaptation and mutation over evolutionary time, resulting in the greatest phenotypic divergence being between the groups that have been the most isolated from one another. Further, as the processes underpinning sexual dimorphism in *Podarcis* lizards are present on the population level (intrasexual combat or copulatory bites; Gvozdík & Van Damme, 2003; Herrel et al., 1996, 1999), we predict that similar patterns of sexual dimorphism will be observed across scales of evolutionary isolation.

Hypothesis 3 predicts that the basis of the sexual dimorphism observed in hypotheses 1 and 2 is the diverging ways each sex responds to the environment. Specifically, we predict that male phenotypes are primarily impacted by sexual selection, particularly environmental factors such as competition, due to the need to compete for mates. We predict that female phenotypes are less impacted by sexual selection and are primarily impacted by natural selection, such as adaptation to diet. This trend is observed in other lizards (Lopez-Darias et al., 2015; Taverne et al., 2020; Vanhooydonck et al., 2010). As part of this, we predict that differing environmental selective regimes on small islets compared to the main islands of Ibiza and Formentera will affect phenotypes. We predict that small islets will have higher levels of competition (as observed on other Mediterranean archipelagos; Donihue et al., 2023), which will cause higher sexual dimorphism in small-islet populations.

Under hypothesis 4, we predict that form–function–environment dynamics identified under hypothesis 3 predictably build upon themselves from the lowest level of isolation to the highest. We predict that the way that environment affects form and function is predictable across scales of evolutionary isolation, and that these trajectories drive the increasing divergence in phenotype with evolutionary divergence observed under hypothesis 3, as observed in Adriatic *Podarcis* species (Taverne et al., 2021).

Together, these hypotheses allow us to assess whether evolutionary trajectories on lower levels of isolation predictably build upon themselves to form trajectories observed on greater levels, allowing us to asses evolutionary scalability within this diverse clade.

Methods

Study sites and species

Data were collected from the Pityusic Islands in the Balearic Archipelago (Spain) of the Western Mediterranean. Data were collected from a total of 340 *P. pityusensis* lizards, a lacertid endemic to the Pityusic Islands, inhabiting Ibiza, Formentera, and 42 islets surrounding them, with populations varying markedly in phenotype and ecology throughout their natural range (Pérez-Mellado, 2009) (Figure 1). This includes 13 sites in total; 3 sites from the main island of Ibiza: Es Pouàs (which is a combination of lizards collected close to St Agnès de Corona), Sa Talaia, and Sal Rossa Tower; 1 site from the main island of Formentera: Punta d'Es Trocadors (here-on referred to as Trocadors); and 7 small-islet sites: Bleda Plana (for which both the shoreline and lighthouse populations were sampled), Conillera (for which both the shoreline and lighthouse populations were sampled), Es Vedrà, Espardell, Espartar, Penjats, and Sal Rossa. Bite force and morphology measurements were taken from sites during September and October 2022 and May 2023, during the breeding season of these lizards (see Dryad dataset, Woodgate et al., 2025). Data were processed to remove lizards that did not complete three bite trials or that did not have all morphometric measurements taken, leaving a total dataset of 307 lizards (see Dryad dataset, Woodgate et al., 2025). Sexes were not sampled equally at each location (see Dryad dataset, Woodgate et al., 2025). Five or fewer females were sampled in Es Pouàs and Trocadors, so some sections of analysis exclude these populations, as signposted in the text. Only adult lizards were sampled; lizards were identified as adults by either size, the presence of copulation marks (females), or developed hemipenes (males).

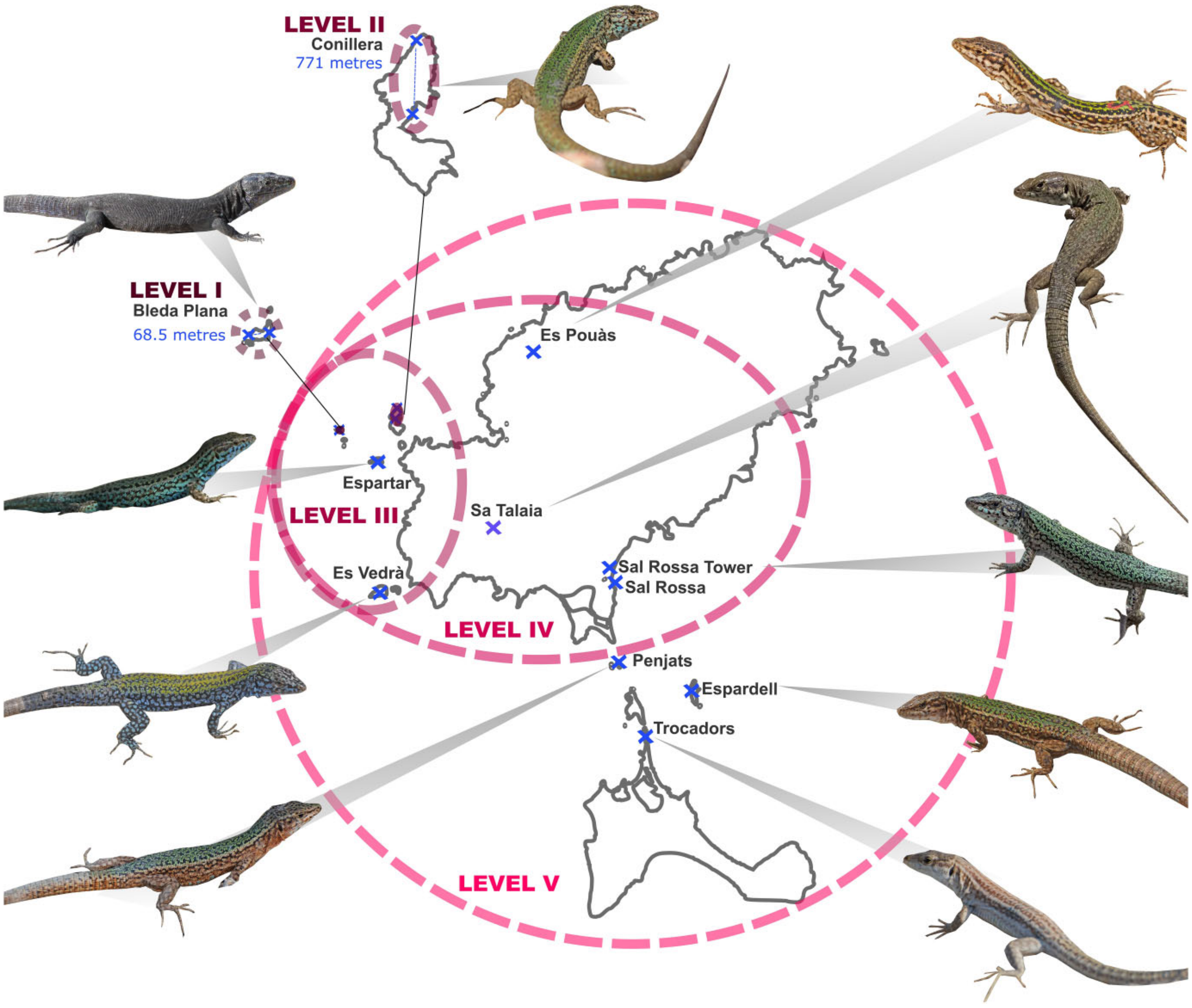

Figure 1. Map of the Pityusic Islands, with locations from which lizards were sampled marked with a cross. For Conillera and Bleda Plana, a measured distance between the shoreline and lighthouse populations is displayed. Dashed circles display the different levels of isolation investigated, as labeled. Map created and distances measured from EMODnetMapViewer, https://emodnet.ec.europa.eu/geoviewer/, content of which is owned by the EU and licensed under Creative Commons CC-BY 4.0 license, https://creativecommons.org/licenses/by/4.0/. A candidate lizard from each population is shown, not to scale; Espartar lizard photo ©Johannes Müller, all other photos ©Ana Pérez-Cembranos.

Populations were classified into five scales of evolutionary isolation (Figure 1), specified as:

Level I: Two populations on Bleda Plana (estimated 68.5 m apart).
Level II: Two populations on Conillera (estimated 770 m apart).
Level III: Four populations on islets Bleda Plana, Conillera, Espartar, and Es Vedrà (combining lighthouse and shoreline data in each of Bleda Plana and Conillera).
Level IV: Eight populations within Clade A, originating from Ibiza (as defined by Rodríguez et al., 2013): Bleda Plana, Conillera, Espartar, Es Vedrà, Es Pouàs Sa Talaia, Sal Rossa, and Sal Rossa Tower.
Level V: Two major clades, separated from one another between 0.1 and 0.3 million years ago, defined by Rodríguez et al. (2013), as follows: Clade A, Ibiza and associated islets; Clade B, Formentera and associated islets.

Data collection

Lizards were captured through lassoing. Bite force data were gathered according to the methods and device described in Herrel et al. (2001) using a Kistler piezoelectric force transducer 9217A, a Kistler force amplifier 5995A, a Kistler cable 1631C1, and a Mitutoyo micrometer 150–801. Each lizard performed three bite force trials (see Dryad dataset, Woodgate et al., 2025), with a "rest period" of roughly 30 min to 1 hr in between to allow muscle strength recovery; during this time, lizards were kept in individual linen bags in semi-shaded, semi-sunlit locations to allow for temperature regulation.

Gape angle is an important factor affecting bite force in vertebrates (Kaczmarek & Gidmark, 2020; Meyers et al., 2018; Santana, 2016). The distance between bite plates was adjusted to provide a standardized gape angle of approximately 35°. Actual gape angle was then estimated by taking an image of one lizard of each sex at each location biting onto the bite plates; measurement of gape angle in these images was then taken using the Angle tool on ImageJ (2012) (see Dryad dataset, Woodgate et al., 2025).

Morphometric measurements were taken with a steel rule and digital calliper to the closest 0.01 mm: snout–vent length (SVL), intact tail length, left hind leg length, and head measurements: head height (HH), pileus length (PL: the distance from the tip of the snout until the posterior margin of the parietal scale), pileus width (the lateral distance between the edges of the parietal scales), and mouth width (the lateral distance at the widest point of the head). Body weight was also measured using a Pesola dynamometer. After measurement, lizards were released at the site of capture.

The presence of digit amputations and regrown or shed tails was also documented. Digit amputation is taken as a proxy for intraspecific competition, as *Podarcis* lizards use biting as a major form of combat (Donihue et al., 2016). Presence or absence of amputation was taken by checking for any missing phalanges, digits, hands, or feet. Tail autotomy reflects both intraspecific aggression and predation pressure, as it is one of the main defenses in lacertid lizards (Arnold, 1988); this was measured by checking for presence and length of regenerated tails.

Ecology

Population density was estimated via line transects. Transects were conducted during the daily period of maximal activity of the lizards (06:30 to 08:30 GMT). During transects, all lizards detected within a strip of 2 m to both sides of the line transect were recorded. Densities, as number of individuals per hectare (see Dryad dataset, Woodgate et al., 2025), were later estimated with N-mixture models using the *unmarked* R package (Fiske & Chandler, 2011). The model of abundance from distance sampling with the fitting function distsamp() was used, which fits the multinomial Poisson model to distance sampling data (2004). The probability of detection for lizard densities was modeled as a function of the distance (d) to the observer using the half-normal detection function (Fiske & Chandler, 2011).

Area and altitude data of each location were retrieved from Lluch i Dubon (1997), a literature search and Google My Maps (see Dryad dataset, Woodgate et al., 2025). To create a single metric of insular habitat availability, maximum altitude (S) and surface area (a) of each island were combined to form a "biotic index" metric, defined as $D = \log(Sa)$ (Cheylan, 1992; Parlanti et al., 1988). No attempt was made to measure islet isolation, as the Pityusic Islands are connected by shallow channels, which were variably exposed during periods of sea level rise and fall during the Pliocene and Pleistocene; it is therefore unknown to what extent nearby islet *P. pityusensis* populations have been truly isolated from one another (Rodríguez et al., 2013). Indeed, a reliable phylogenetic tree is not currently available for this species; genetic analysis has found a mixed picture of relationships between populations, with polytomies and differing relatedness depending on the part of the genome investigated (Pérez-Mellado et al., 2017; Rodríguez et al., 2013), likely due to high levels of admixture throughout the evolutionary history of this species.

Diet data were collected from analysis of fecal samples following methods set out in Pérez-Cembranos et al. (2016). Fecal samples were collected from lizards which presented them at each location. Data were combined with data from previous field "extended summer" seasons to get a longer-term representation of diet (see Dryad dataset, Woodgate et al., 2025). Feces were analyzed under a binocular microscope; abundance and type of food items contained therein were identified to the order level. Percentage frequency of plant matter and percentage frequency of *Podarcis* remains were directly included in the dietary analysis. To calculate the percentage frequency of hard foods, each food item was classified into "hard" or "soft" according to Donihue (2016) and Vanhooydonck et al. (2007) and our own knowledge for those not included therein (see Dryad dataset, Woodgate et al., 2025). Dietary diversity was assessed using Hill's numbers, which were generated for each population using the function hill_taxa() from the package *hillR* (Li, 2018). Hill's numbers are used because they can be considered "true" diversity indices, more straightforward for interpretation and comparison than "raw" diversity estimates such as the Simpson or Shannon indices (see Pallmann et al., 2012, for further discussion). The function mcpHill() from the package *simboot* (Scherer & Pallmann, 2014) was used to test whether dietary diversity differed between populations. This shows that some populations significantly differ from one another in dietary diversity (Supplementary Table 1), so Hill $q = 2$ values, which represent the inverse Simpson index, are taken as estimates for diversity of prey, referred to as "dietary diversity" throughout the rest of the study (see Dryad dataset, Woodgate et al., 2025).

Initial data treatment

All data analysis was performed on R. For each lizard, the maximum bite force of all trials is used in the analysis. Body temperature was not recorded at the time of biting, so strength of bite during each trial was analyzed in order to discern whether possible muscle fatigue or body temperature fluctuation affected bite force. The maximum bite recorded for each lizard was evenly distributed between trials (Supplementary Table 2). A Spearman correlation between average and maximum bite force across all three trials fitted using the function cor.test() from the package *stats* (R Core Team, 2023), gave Spearman's $\rho = 0.9942$, $p < 2.2\mathrm{e}{-16}$, suggesting that muscle fatigue and temperature had negligible effect on bite force, and thus will not be controlled for throughout the rest of the study.

All bite force and morphometric data were natural log-transformed to better facilitate allometric comparisons (Houle et al., 2011; Runemark et al., 2015) and to account for skew in the data.

Before further analysis, structure of the data was assessed. Shapiro–Wilk tests were performed using the function shapiro.test() from the package *stats* to check whether bite force and linear morphology measurements are normally distributed. Levene's tests were performed using the function leveneTest() from the package *car* (Fox & Weisberg, 2019) to check for homogeneity of variances (Supplementary Table 3). Some metrics show nonnormality and/or nonhomogeneity of variances. For this reason, methods that do not assume normality or homogeneity of variances are employed throughout the analysis.

To test whether gape angle determines bite force, linear models for each sex were generated of log-transformed gape angle against log-transformed bite force using the function lm.rrpp.ws() from the package *RRPP* (Collyer & Adams, 2018, 2024), where population was specified as subject. This is because estimated gape angle was measured once for either sex at each location. This fits an ordinary least-squares linear model based on 1,000 permutations and does not assume normality or homogeneity of variances. Significance of variables was then assessed by performing ANOVAs on these fitted models using the function anova() (Supplementary Table 4). As gape angle does not impose a significant control on bite force, it is not controlled for throughout the rest of the analysis.

Data analysis

The form–function relationship in *P. pityusensis*

To investigate whether males are morphologically different to females, linear models were fitted using the function lm.rrpp() with 1,000 permutations based on the entire dataset, on which ANOVAs were performed. In the first, logSVL was specified as the dependent variable and sex as the independent variable. In the second, all log head shape variables were specified as dependent variables, and interaction of sex and logSVL as independent variables. To test which morphology metrics underpin bite force, an lm.rrpp() model was fitted with log bite force as the dependent variable and a three-way interaction between logSVL, sex, and all head metrics as independent variables.

Form–function relationships across scales

Phenotypic divergence was investigated across levels of evolutionary isolation by generating the same lm.rrpp() models described under hypothesis 1 for each level, with "Group" (i.e., isolation extent) included as an independent variable. At levels I, II, III, and IV, the group is the population the lizard originated from, and at level V, the group is clade. For isolation levels IV and V, location Es Pouàs (and Trocadors in the case of level V) was removed from any dataset including females due to low sample size.

The form–function–environment relationships in *P. pityusensis*

To assess whether lizards from small islets are larger and have a greater bite force than lizards from main islands, populations Sa Talaia and Sal Rossa Tower are classified as "main island" (Es Pouàs and Trocadors were excluded), and all others classified as small-islet populations. Linear models based on 1,000 permutations using the function lm.rrpp.ws() were created, with population specified as subject, so each individual lizard is treated as an observation within its population, given that each population has just one value for islet habitation. In the first model, bite force was the dependent variable, and sex, islet, and their interaction, alongside logSVL, were the independent variables. In the second model, logSVL was the dependent variable, with sex, islet, and their interaction as the independent variables. In the third model, all log head shape metrics were the dependent variables, and sex, islet, and their interaction alongside logSVL were the independent variables. ANOVAs were then performed on these models, the results of which are analyzed next. Wilcoxon tests were run to test whether insularity covaried with specific environmental variables using the function wilcox.test().

Next, the association between phenotype and specific environmental variables was investigated. To investigate environmental associations with form–function evolution, the function lm.rrpp.ws() was used to create linear models with log bite force as the dependent variable and ecological metrics as independent variables. LogSVL and sex were included as independent variables to account for differences in bite force due solely to size and sex. Population was specified as subject given that every population has just one value for each ecological variable; all ecological variables were averaged for each population, which involved creating "combined" values for lighthouse and shoreline populations of Conillera and Bleda Plana. Es Pouàs and Trocadors were removed from models of levels IV and V. Two different models were initially generated to avoid overfitting. The first was an "abiotic" linear model, with independent variables percentage plant food in the diet, percentage hard food in the diet, dietary diversity, and the biotic index. The second was a "biotic" linear model including independent variables amputation rate, tail autotomization rate, log-transformed population density, and percentage cannibalism in the diet. ANOVAs were performed to test the significance of each variable on the dependent variables; any variable with a significant z-value ($p < 0.05$) in the "biotic" or "abiotic" models was then incorporated into a "total environment" linear model. ANOVAs were then performed again to test the significance of each of the "total environment" variables; any variable with a significant z-value ($p < 0.05$) was then incorporated into a "final" model, the results of which are analyzed later. This extra step of creating a "final" model was performed because some "total environment" models retained so many variables that they had errors related to overfitting.

The same linear model procedure, beginning with "biotic" and "abiotic" models to contribute to a "final" environmental model, was then repeated with logSVL as the independent variable, to investigate how environmental variables are associated with body size.

Form–function–environment relationships across scales

To test whether environmental drivers on patterns of bite force and size sexual dimorphism are scaleable, lm.rrpp() models described earlier were created with datasets of lizards from levels III, IV, and V, with "Group" (i.e., isolation extent) specified as subject. For female datasets of isolation levels IV and V, location Es Pouàs (and Trocadors in the case of level V) was removed. The same was also performed with average log SVL as an independent variable, to investigate scalability of form–environment relationships.

Results

Morphological underpinnings of bite force

Male *P. pityusensis* lizards are larger than females, with a larger head (Supplementary Tables 5 and 6; Figure 2C–E). Males also bite harder than females (Supplementary Table

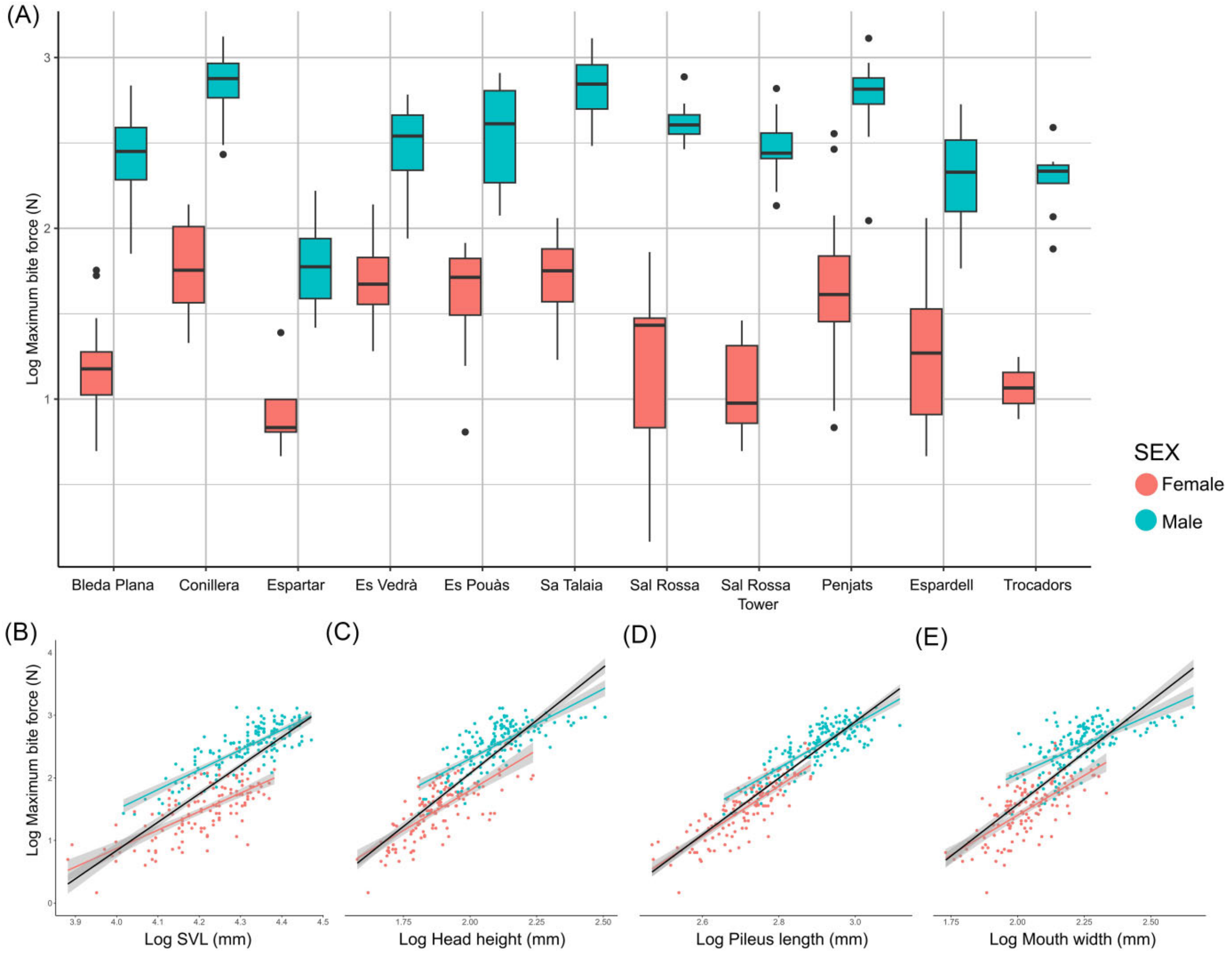

Figure 2. (A) A boxplot of the log maximum bite force completed by each lizard at each location. Females are shown in red and males in blue. (B–E) Sexual dimorphism in form–function relationships, displaying how morphological factors underpin bite force. Red lines represent females and blue lines represent males; each point represents one individual. Relationship of both sexes combined shown in black. Gray bars represent standard error.

7; Figure 2A and B). ANOVAs on a model of total dataset bite force reveal that SEX, logSVL, logHH, and logPL all significantly determine bite force, alongside the interactions sex:logPL, logSVL:logHH, and three-way interactions sex:logSVL:logHH, and sex:logSVL:logPL (Supplementary Table 7). This displays that each sex has significantly different bite force and different morphological underpinnings of bite force.

Morphological underpinnings of bite force across scales

There is significant sexual dimorphism in body size, head shape, and bite force across isolation scales investigated (Supplementary Tables 5–7). SVL diverges between populations only at levels III and IV, and further, at level IV, populations diverge in the extent of sexual dimorphism in SVL, as the interaction of sex:location has $p < 0.05$. Head shape diverges between populations at all levels of evolutionary isolation apart from level V, and all isolation levels report groups with similar extent of head shape sexual dimorphism. Bite force diverges between groups at isolation levels I, III, and IV, but not at levels II or V; indeed, groups also have differing extents of bite force sexual dimorphism at levels III and IV, but not at level V. Therefore, the two major clades have similar phenotypes, despite greater divergence at smaller scales.

The morphological underpinnings of bite force are less incongruous across scales; body size and all head shape metrics are significantly associated with bite force across isolation levels, with greater significance of interactions between sex and morphology metrics as isolation scales increase.

Form–function–environment relationships in *P. pityusensis*

Populations from small islets have a significantly greater body size than those from the main islands; however, there is no difference in bite force or head shape when controlling for body size (Table 1). There is also no significant difference in extent of sexual dimorphism between the small islets and main islands in any phenotypic metric; this is despite the fact that small-islet habitats have significantly higher population

Table 1. Summarizing results of ANOVAs based on linear models describing whether phenotype is determined by inhabiting a small islet.

Dependent variable	Independent variable	*df*	SS	MS	Rsq	*F*	*Z*	*Pr*(>*F*)
Log bite force	Islet	1	0.164	0.1643	0.00141	2.4102	1.2075	0.121
	SEX	1	17.903	17.9025	0.15361	262.6617	7.6157	0.001***
	log(SVL)	1	12.69	12.6899	0.108884	186.1828	6.9831	0.001***
	Islet:SEX	1	0.001	0.001	0.000009	0.0153	-1.3821	0.905
	Residuals	271	18.471	0.0682	0.158487			
	Total	275	116.545					
	Final				0.8415134	359.7308	18.42371	0.001***
Log SVL	Islet	1	0.6345	0.63451	0.19229	119.9669	6.4885	0.001***
	SEX	1	1.2443	1.24433	0.37709	235.2632	6.9128	0.001***
	Islet:SEX	1	0.0145	0.01445	0.00438	2.7325	1.2277	0.104
	Residuals	272	1.4386	0.00529	0.43598			
	Total	275	3.2998					
	Final				0.5640219	117.2948	11.52555	0.001***
Log head shape	log(SVL)	1	7.586	7.5856	0.140543	175.3728	6.6001	0.001***
	Islet	1	0.028	0.0278	0.000516	0.6436	0.2748	0.394
	SEX	1	4.912	4.912	0.091008	113.5617	5.8521	0.001***
	Islet:SEX	1	0.026	0.0261	0.000484	0.6039	0.2543	0.421
	Residuals	271	11.722	0.0433	0.217178			
	Total	275	53.974					
	Final				0.7828218	244.2058	17.1957	0.001***

Note. SVL = snout–vent length, *df* = degrees of freedom, SS = sum of squares, MS = mean squares, Rsq = R-squared. Significance of *p* values is highlighted with asterisks.

density and lower biotic index compared to the main islands (Supplementary Table 8).

Across the entire dataset, bite force is determined by sex, population density, and rate of tail autotomy (Table 2) and SVL is controlled by the same factors including biotic index (Supplementary Table 9).

Form–function–environment relationships across scales

At level III, male bite force is significantly associated percentage hard food only (Table 2). At level IV, percentage plant food and dietary diversity significantly impact male bite force. At level V, population density and percentage hard food are associated with male bite force. There is therefore a shift in the environmental factors controlling male bite force as the scale of evolutionary isolation increases from levels IV to V—from habitat alone to habitat and competition.

At level III, population density, percentage cannibalism, and amputation rate are significantly associated with female bite force (Table 2). At level IV, no environmental variables can be linked to female bite force, while at level V, female bite force is significantly associated with biotic index. Similar to males, there is clearly a shift in the environmental factors controlling female bite force as the scale of evolutionary isolation increases, from competition drivers to habitat.

At level III, all competition metrics are significantly associated with male SVL (Supplementary Table 9). At level IV, population density, amputation rate, and tail autotomization rate impact male SVL. At level V, male SVL is associated with population density, tail autotomization rate, percentage plant food, and biotic index. At level III, population density, percentage cannibalism, and tail autotomization rate are associated with female SVL (Supplementary Table 9). At level IV, biotic index is the only environmental variable impacting female SVL. At level V, population density, percentage plant food in the diet, and biotic index control female SVL. Thus, in both sexes, at smaller scales, body size is driven by competition, while at larger scales of isolation, SVL is driven by a combination of competition and habitat.

Discussion

Results presented here show that precisely how form drives function in *P. pityusensis* differs between sexes and across levels of evolutionary isolation. The same is true for the manner in which environmental factors impact bite force and body size; there is incongruence in form–function–environment relationships across evolutionary scales. Phenotype increasingly diverges as populations become more isolated up until the greatest isolation level, the two major clades, between which there is no phenotypic divergence. Microgeographic divergence in *P. pityusensis* thus does not predictably scale upwards.

Sexual dimorphism in form and function

Our results show that male *P. pityusensis* lizards have a higher bite force, larger body size, and larger head than females across scales of isolation, meaning that hypothesis 1 can be accepted. The trend of a larger body, head, and bite force in males is observed in diverse lizard groups (Herrel et al., 2001, 2007; Li et al., 2023; Sagonas et al., 2014), including other *Podarcis* species (Brecko et al., 2008; Gomes et al., 2018; Kaliontzopoulou et al., 2012; Patti et al., 2023; Verwaijen et al., 2002).

Sexual dimorphism in form and function across scales

The lack of phenotypic divergence in major clades of *P. pityusensis* is despite greater disparity on smaller evolutionary scales. Difference in SVL between groups is only significant at evolutionary isolation levels III and IV, while head shape diverges between groups at levels I, II, III, and IV. Function shows similar incongruence across scales; bite force di-

Table 2. Summarizing results of ANOVAs based on linear models of the relationship between environmental variables and bite force.

Dependent variable	Independent variable	*df*	SS	MS	Rsq	*F*	*Z*	*Pr*(>*F*)
All populations log bite force	SEX	1	20.29	20.2905	0.1741	343.079	7.8321	0.001***
	log(SVL)	1	16.459	16.459	0.141224	278.296	7.3909	0.001***
	Population density	1	1.888	1.8877	0.016197	31.918	4.0194	0.001***
	Overall tail autotomization rate	1	1.876	1.8758	0.016095	31.716	4.0144	0.001***
	Residuals	271	16.028	0.0591	0.137522			
	Total	275	116.545					
	Final				0.86248	424.8978	18.5051	0.001***
Level III log male bite force	log(SVL)	1	1.0122	1.01221	0.13845	27.824	3.7505	0.001***
	Percent hard diet	1	1.1764	1.17641	0.16091	32.338	3.9124	0.001***
	Residuals	83	3.0194	0.03638	0.413			
	Total	85	7.311					
	Final				0.587	58.98517	7.606332	0.001***
Level IV log male bite force	log(SVL)	1	12.6297	12.6297	0.56218	317.4325	7.9427	0.001***
	Percent plant diet	1	0.3949	0.3949	0.01758	9.9248	2.5187	0.002***
	Dietary diversity	1	0.2807	0.2807	0.01249	7.055	2.1368	0.009**
	Residuals	141	5.61	0.0398	0.24971			
	Total	144	22.4657					
	Final				0.75029	141.216	11.38519	0.001***
Level V log male bite force	log(SVL)	1	11.6512	11.6512	0.47867	295.9693	7.5438	0.001***
	Population density	1	0.2085	0.2085	0.00857	5.2975	1.8793	0.022*
	Percent hard diet	1	1.2077	1.2077	0.04962	30.6786	3.8377	0.001***
	Residuals	171	6.7316	0.0394	0.27656			
	Total	174	24.3406					
	Final				0.72344	149.104	13.5848	0.001***
Level III log female bite force	log(SVL)	1	2.163	2.16295	0.24148	40.247	4.4379	0.001***
	Population density	1	0.5703	0.57028	0.06367	10.612	2.4526	0.003***
	Cannibalism	1	1.222	1.222	0.13643	22.738	3.3121	0.001***
	Female amputation rate	1	0.5377	0.53771	0.06003	10.005	2.5798	0.003***
	Residuals	67	3.6007	0.05374	0.402			
	Total	71	8.9569					
	Final				0.598	24.9168	7.619647	0.001***
Level IV log female bite force	log(SVL)	1	7.9433	7.9433	0.44567	87.711	5.4808	0.001***
	Biotic index	1	0.2956	0.2956	0.01659	3.2644	1.4447	0.07
	Residuals	104	9.4185	0.0906	0.52844			
	Total	106	17.8232					
	Final				0.47156	46.40276	6.663781	0.001***
Level V log female bite force	log(SVL)	1	10.8934	10.8934	0.49441	122.3899	6.0956	0.001***
	Biotic index	1	0.4818	0.4818	0.02187	5.4135	1.8417	0.02*
	Residuals	122	10.8587	0.089	0.49284			
	Total	124	22.0331					
	Final				0.50716	62.7733	7.29703	0.001***

Note. SVL = snout–vent length *df* = degrees of freedom, SS = sum of squares, MS = mean squares, Rsq = R-squared. Significance of *p* values is highlighted with asterisks.

verges between populations at levels I, III, and IV. Therefore, despite divergence in form and function even at the very lowest levels of evolutionary isolation, there is no divergence in phenotype between major clades.

The significant divergence of head shape and bite force between populations at isolation level I is despite these populations being only an estimated 68.5 m (measured on EMODnetMapViewer, Figure 1) apart. While this may be due to developmental plasticity or random phenotypic variation, it may also reflect extreme microevolutionary adaptation to local environment, as such a short distance is likely within the range of these lizards (as measured in other insular *Podarcis* species; Swallow & Castilla, 1996; Verwaijen & Van Damme, 2008). This is especially interesting as lizards at level II diverge in head morphology but not bite force; the distance between these populations is an estimated 771 m (measured on EMODnetMapViewer, see Figure 1), unlikely to be within range of these lizards. This may suggest that conditions are more similar over the entire islet of Conillera than over the islet of Bleda Plana; unfortunately, our current dataset precludes testing of environmental drivers at both locations on these islets. This divergence in phenotype within small islets mirrors findings of diverging head morphology in less than 1 km spanning the shoreline to inland in *Teira dugesii* lizards of Madeira (Brown et al., 2023), in populations with clear evidence of gene flow. We therefore suggest that *P. pityusensis* populations show adaptation in phenotype to their local environment, even on extremely small scales. Overall, we must reject hypothesis 2; while phenotypic divergence increases with increasing isolation across levels III to IV, the lack of phenotypic divergence between major clades means that microgeographic diversity is not evolutionarily scalable.

Form–function–environment relationships across scales

Environment drives form–function relationships in both sexes of *P. pityusensis*. Islet individuals are larger than main island lizards, but bite force and head shape are not significantly different (when controlling for body size). This may be due to the higher population density on islets potentially causing higher intraspecific competition. Other factors such as founder effects or demographic differences could have an effect on islet lizard phenotypes; as discussed in the *Methods* section, genetic analysis leaves an unclear picture of the precise isolation or colonization of each islet (Rodríguez et al., 2013). The trend of larger lizards on islets is also seen in other *Podarcis* species, such as *P. gaigae* (Runemark et al., 2015), although in this case size change is linked to dietary shifts. *Podarcis pityusensis* does not display dietary divergence according to insularity; our observations therefore fit more closely to trends observed in *P. erhardii* in which higher levels of intraspecific competition on small-islet environments drive an increase in body size and bite force, even in absence of dietary divergence (Donihue et al., 2023).

There is incongruence in how specific environmental variables influence phenotypes across scales. In females, competition is a more important driver at levels of lesser isolation, while habitat is more important at greater levels. In males, habitat has a stronger influence on phenotype at levels of lesser isolation, while competition has a stronger influence at greater levels. We are therefore able to accept hypothesis 3. Overall, habitat is the most important driver of female form and function, with biotic index and percentage plant food being the individual environmental factors with the greatest effect on female phenotype. Both competition and habitat have significant effects on male form and function, with population density, tail autotomization rate, percentage plant food, and percentage hard food in the diet enacting the greatest influence on male phenotype.

The association of plant and hard food with male and female phenotypes suggests that bite force determines the extent to which lizards can access food resources, which are tough to break down—foods which Balaeric lizards are noted for specializing upon (Pérez-Mellado & Corti, 1993).

Tail autotomization rate reflects both intraspecific (combat between lizards, which amputation rate also reflects) and interspecific (predation) aggression. The main predators of *P. pityusensis* are visiting kestrels, seagulls, and owls (Cooper & Pérez-Mellado, 2012). Work relating predator abundance to lizard adaptation usually focuses on body size; for example, in their meta-analysis of global urban lizard populations, Putman and Tippie (2020) suggest that larger lizards may be better able to evade predators (especially cats), yet conversely, Stadler et al. (2022) found evidence for smaller female *P. erhardii* lizards on Aegean islets with resident birds of prey. While in *P. pityusensis*, tail autotomization is significantly associated with male body size, it is less associated with female body size (only significant at level III). This suggests that tail autotomization is not a metric solely recording levels of predation in the system, as males and females follow different trends. For these reasons, we suggest interpretation of tail autotomization as a measure of overall aggression in the system, i.e., both inter- and intraspecific combat, alongside amputation rate.

Aggression is often tightly linked to competition within a system, which can be linked to population density; population density is also significantly associated with male *P. pityusensis* bite force and body size. A possible mechanism is that higher densities may lead to higher sexual competition, either inter- or intrasexual competition, or a combination of both (Gvozdík & Van Damme, 2003). However, our result that higher population densities on small-islets do not lead to higher sexual dimorphism compared to the main islands suggests that this should be interpreted with some caution. Indeed, it should be considered that this study contains only proxies for aggression, that behavioral survey would be necessary to fully confirm that aggression is different in different populations. However, interisland variation of intraspecific competition and aggression in *Podarcis* is well-documented, such as in *P. siculus* (Vervust et al., 2009). Levels of aggression and competition are known to be important in form–function evolution in other lacertids; higher competition is associated with larger body size in *P. gaigeae* (Pafilis et al., 2009) and higher aggression and bite force in *P. erhardii* (Donihue et al., 2016, 2023), with evidence that greater body size and bite force are associated with winning intraspecific contests in *P. erhardii* (Brock et al., 2020, 2022) and *Gallotia galloti* (Huyghe et al., 2005). We therefore suggest that the association of male *P. pityusensis* phenotypes with aggression on the largest scales may be due to sexual selection, under which greater bite force confers greater chances of winning male–male combats and successful copulatory biting.

Incongruence in evolutionary scaling of form–function–environment relationships

While microevolutionary divergence between sexes and populations of *P. pityusensis* is clear, there is no divergence in phenotype at the greatest level of isolation, i.e., between major clades, despite being separated from one another for over 100,000 years (Rodríguez et al., 2013). Further, the way in which form drives function depends on the evolutionary scale investigated. This incongruence between evolutionary scales is different to other works; for example, Taverne et al. (2021) find that in *Podarcis* species of the Adriatic, local selective pressures drive microgeographic variation, which can impose predictable patterns of form–function evolution up to the interspecific level, which they interpret as a link between micro- and macroevolution. Our results are contrary, i.e., extreme microevolutionary adaptation in phenotype is observed at level I (in terms of head shape and male bite force), yet is nonexistent at level V; further, how specific environmental selective pressures drive form and function differs at levels III, IV, and V. We therefore must reject hypothesis 4.

In *P. pityusensis*, phenotypic diversity does not predictably scale with evolutionary isolation, meaning that environmental selective pressures do not have predictable effects on form, which do not cause predictable changes in function that can be traced throughout scales of evolutionary isolation. Perhaps plasticity is the reason for the apparently higher levels of phenotypic variation on smaller isolation scales. *Podarcis pityusensis* lizards may flexibly alter their phenotype during ontogeny to best suit their environmental surroundings, which would be one explanation of the great diversity on smaller scales, which does not build toward overall divergence. The problem of discerning plasticity from adaptation in the natural world is a contentious one and can only be properly assessed via genetic analysis of populations; we suggest that this could be a fruitful next step for this work.

Overall, it is clear that evolutionary patterns in *P. pityusensis* observed over the smallest scales cannot be translated to those on the largest. Rather, we suggest that at level V, phenotype is "stabilized," masking greater phenotypic variation observed at lower levels and suggesting that populations are more strongly influenced by local environmental selective pressures than phylogenetic history. More empirical work must be done to elucidate why some species such as *P. pityusensis* do not show any evidence of reproductive isolation in association with phenotypic divergence, and why others do begin speciation, as appears to be case for the Adriatic *Podarcis* species. High levels of developmental plasticity in *P. pityusensis* may be the answer; if so, then it begs the question why this species is able to undergo a higher level of plasticity compared to others in the genus.

Conclusion

In a highly comprehensive analysis linking form, function, and environment of a single species, we find incongruence in evolutionary trajectories as the level of evolutionary isolation increases. Phenotypic divergence is observed on extremely small scales, but at the scale of greatest isolation, between clades separated 0.1 million years ago, no divergence is observed. Natural selection appears to be the prevailing force in female form–function evolution, while males appear shaped by a mixture of natural and sexual selection; however, form–function–environment relationships vary depending on the scale of isolation investigated. In total, environmental selective pressures do not drive predictable changes in form, and changes in form do not drive predictable changes in function, which can be translated across scales. The great microgeographic diversity in *P. pityusensis* thus does not build toward macroevolutionary divergence, perhaps as a result of high developmental plasticity in this species. This work thus displays how microevolutionary divergence can be masked on more macroevolutionary scales, highlighting the critical importance of empirical studies of intraspecific variation for our understanding of evolution.

Supplementary material

Supplementary material is available online at *Evolution*.

Data availability

Data and R script are archived in Dryad, accessed via: DOI: https://doi.org/10.5061/dryad.hhmgqnkt8

Author contributions

S.C.W., A.P.-C., V.P.-M., and J.M. conceived the study, collected the experimental data, discussed the results, and contributed to the final manuscript. S.C.W. conducted the statistical analysis and drafted the manuscript.

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Conflict of interest

The authors declare no conflict of interest.

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