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ORIGINAL RESEARCH

Environmental drivers of scale morphology in a Canary Island lizard across 3700 m of elevation

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Abstract

The skin serves as the outermost barrier between an organism and its environment and fulfills numerous physiological and ecological functions. In lizards, scale morphology is an important adaptive trait that mediates responses to environmental influences such as extreme temperatures, ultraviolet radiation, drought and anthropogenic disturbances. Our study provides an analysis of the environmental drivers influencing intraspecific variation in the scale ecomorphology of the island lizard *Gallotia galloti* across 3700 m of elevation, taking into account different macro- and microclimatic conditions and varying degrees of anthropogenic influences and across three body regions: dorsal, ventral and tail. We found several correlations suggesting multiple dependencies of scale morphology on environmental variation. The positive correlation between July temperature and wind speed at 3 cm above the ground and dorsal scale density showed that more densely packed scales are associated with hotter and drier environments. This could possibly be related to the thermoregulatory and hydroregulatory function of the skin, since the dorsal side of the body is most exposed. Higher sun exposure was associated with larger dorsal and tail scales, indicating a possible photoprotective function. Ventral scales are not exposed to the pressure of solar radiation and wind. Accordingly, ventral scales showed no correlation with these factors, but we found that a higher ratio of day-to-night temperature variation relative to seasonal changes (isothermality) was associated with a higher density of ventral scales. The human footprint index positively correlated with larger and denser ventral (and not dorsal or tail) scales. Overall, our results illustrate the complexity of responses of scale morphology to different environmental variations. Evidently, *G. galloti* exhibits morphological diversity in response to climatic conditions and urbanization, highlighting the potential ecological significance of scale size variation. Future research should investigate the genetic basis and possible effects of climate change on scale morphology.

Introduction

Ecomorphology investigates the relationship between the morphology of an organism and its ecological function in relation to the environment (Wainwright & Reilly, 1994). It examines how structural adaptations influence survival, reproduction and general fitness, something that has been extensively studied in different groups of organisms (Barr, 2018; Bock, 1994; Miles & Ricklefs, 1984) including in lizards (Losos, 1990; Vanhooydonck et al., 2006). Ectothermic vertebrates, including lizards, are sensitive to thermal and hydric fluctuations in the environments where they occur. To buffer these fluctuations, they use different strategies, including adaptations in their integument, which is a barrier that minimizes temperature and water exchange between the inner body and the surrounding air (Dmi'el, 2001; Lillywhite, 2006). Besides that, the skin of lizards has other important functional roles, such as protection against physical damage, crypsis or enhancing locomotion (Vitt & Caldwell, 2013).

In lizards, the outer layer of the skin is constituted by keratinized scales of variable size, shape and texture (Rutland et al., 2019), which can vary between and within species. Scale morphology of lizards has been found to be shaped by environmental factors such as temperature, humidity and ultraviolet (UV) radiation (Oufiero et al., 2011; Soulé & Kerfoot, 1972; Tulli & Cruz, 2018; Wegener et al., 2014). For example, in environments with high UV exposure, denser and smaller dorsal scales may provide a photoprotective advantage, while larger scales may help minimize water loss in arid conditions (Oufiero et al., 2011). Moreover, skin is the main organ involved in the regulatory processes of water loss in Mautz (1980). Lizards' outer epidermis, composed of keratin, is formatted in scales (Tulli & Cruz, 2018). Scales vary in shape, size, texture, colour and density at both intraspecific levels and between differing body regions within the same individual (Rutland et al., 2019; Wegener et al., 2014). Dorsal scales typically possess greater thickness and vary in size (Wegener et al., 2014). In contrast, ventral scales tend to be large, smooth and flat, facilitating locomotion and providing protection against injury, particularly as the ventral area of the lizard frequently contacts rough ground surfaces (Rutland et al., 2019). *Anolis* lizards from dry environments have fewer and larger scales than species from humid environments (Wegener et al., 2014). In addition, the number of scales varied among different *Anolis* ecomorphs and correlated with aspects of the structural microhabitat (i.e. perch height and perch diameter) (Wegener et al., 2014). The same authors showed that scale size, shape or texture can vary considerably among populations inhabiting different habitats. Although previous research on scale morphology, particularly in response to environmental variation, exists, it primarily focuses on comparisons across multiple species. Our study is, to our knowledge, the first intraspecific ecomorphological analysis of scales done in lizards.

Elevation gradients feature diverse abiotic conditions as they encompass globally experienced environmental characteristics associated with elevation, including decreases in temperature and increases in solar UV radiation (Körner, 2007). As elevation increases, the impact of the human footprint also generally decreases due to reduced human activities and infrastructure development at higher elevations (Mu et al., 2022). In areas with a high human footprint, organisms may develop traits like smaller body size, altered coloration or other morphological changes to adapt to fragmented habitats, poor habitat quality, pollution, etc. (Falvey et al., 2020; Magory Cohen et al., 2020). Ectothermic vertebrates like lizards inhabit a wide range of environments, including different elevations and a wide range of natural, semi-natural and urban or highly modified landscapes, making them suitable model species to study adaptation to such environmental gradients (González-Morales et al., 2020; Pianka & Vitt, 2003; Serén et al., 2023).

The present study investigated ecomorphological variation in *Gallotia galloti*, a medium-sized (average snout-vent length = ~130 mm; Oppliger et al., 1999) diurnal lizard (Salvador, 2015). This species is endemic to the Canary Islands and is distributed along a steep altitudinal gradient of 3700 m (Speybroeck et al., 2016). Multiple studies have expressed that thermo- and hydroregulation in lizards is affected by climate (Garcia-Porta et al., 2019; González-Morales et al., 2020; Hertz & Huey, 1981; Oufiero et al., 2011), which has also recently been described for *G. galloti* (Serén et al., 2023). By analysing the shed skin samples from lizards captured at different elevations and across diverse environmental conditions (including human footprint), we explore whether intraspecific scale morphology of lizards shows variation in relation to the diverse environmental conditions across elevation. To refine our approach, we observe climate at both the macro- and micro-scale, adding another dimension to our understanding of functional traits involved in local adaptation. The observed variation could be due to local adaptation or plasticity (or adaptive plasticity), although the distinction between these processes would require further research.

The aim of our study is to compare the morphology of dorsal, ventral and tail scales in *G. galloti* from populations with diverse climatic and habitat conditions across a 3700 m elevation span. Firstly, we predict that scale morphology will vary across body regions (Rutland et al., 2019) and in response to changing temperatures across the elevation span (Tulli & Cruz, 2018). Secondly, we assume that increasing UV radiation will act as a pressure on dorsal scale density variation and size. We expect to observe an increase in dorsal scale density and size reduction as a photoprotective mechanism to the increasing UV radiation at elevations above 2000 m above sea level (a.s.l.) because previous studies identified this as an elevation threshold associated with selective pressure (Reguera et al., 2014; Serén et al., 2024). Thirdly, we expect that areas with a high human footprint may represent altered habitats and may be correlated with changes in morphology compared to natural populations (Gómez-Benitez et al., 2021). Fourth, we predict that scale morphology might be involved in the hydroregulation of this species; thus, in the hotter and drier areas, we expect to find larger scales regardless of the body region, which would help them to better retain water under such climatic conditions (Dmi'el, 2001). Finally, the inclusion of climate predictors at the macro- and micro-levels will allow us to compare variation in skin morphology under different selection pressures either at a broader or more local level. We hypothesize that both climatic aspects influence scale morphology and the results will identify how these traits vary along an environmental gradient.

Materials and methods

Lizard collection

Shed skin samples of *G. galloti* were collected in August 2021 and April 2023 across 16 sample locations in Tenerife (Canary Islands) (Fig. 1 and Table S1). Sampling comprised locations across elevation from the lowest at 43 m and the highest at ~3650 m a.s.l, the cone of the Teide stratovolcano, which is the highest point of Tenerife Island. Each site was named, and coordinates and elevation measurements were obtained using a GPS (GPSMAP 64 s, Garmin, Kansas, USA) (Table S1). We used between 15 and 30 pitfall traps per sampling site to collect the lizards. They were baited with fruit and set at 10 m intervals from each other in each sampling site, except at the cone of the Teide volcano (location CT – at 3650 m asl) where lizards were captured using a slip-loop (García-Muñoz & Sillero, 2010), due to low abundance (Megía-Palma et al., 2024). In total, we captured over 800 lizards, of which 116 lizards were shedding skin, allowing us to collect shed skin samples. The skin of shedding

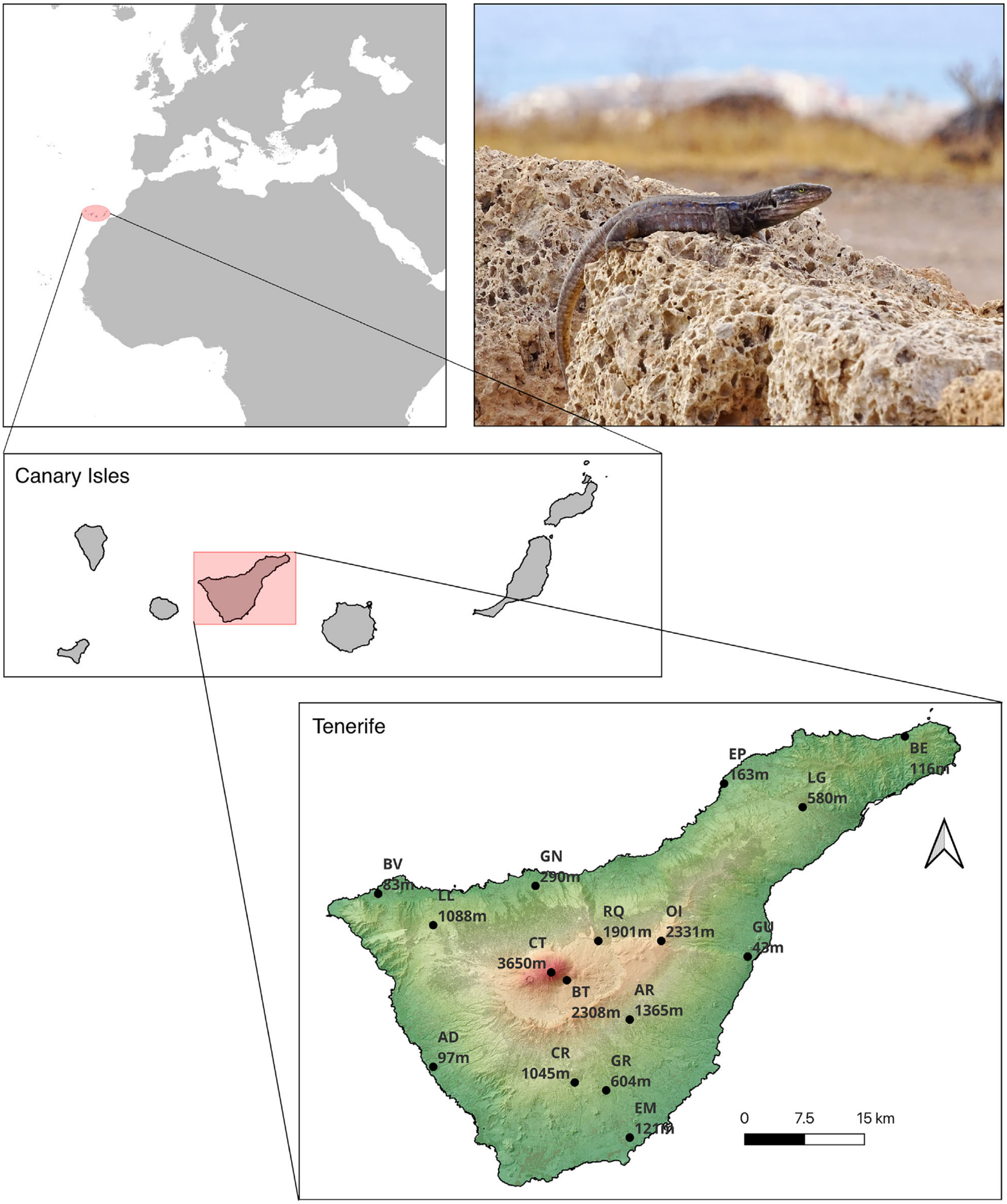
Canary Isles
Tenerife
EP
163m
BE
116m
LG
580m
BV
83m
GN
290m
LL
1088m
RQ
1901m
OI
2331m
GU
43m
CT
3650m
BT
2308m
AR
1365m
AD
97m
CR
1045m
GR
604m
EM
121m
0
7.5
15 km

Figure 1 Sampling of *Gallotia galloti* in Tenerife. The geographic location of the Canary Islands and Tenerife in association with the Canary Islands is presented on the top left and in the middle. The male individual is presented on the top right (photo credits: Miha Krofel). The magnification at the bottom shows the 16 sampling locations of *G. galloti*, with each point including the ID of the location. AD, Adeje; AR, Area Recreativa El Contador; BE, Benijo; BT, Base of Teide; BV, Buenavista del Norte; CR, Cruz de Tea; CT, Cono de El Teide; EM, El Médano; EP, El Pris Mirador de Juan Fernández; GN, La Guancha; GR, Granadilla de Abona; GU, Puertito de Güímar; LG, La Laguna; LL, San José de Los Llanos; OI, Izaña astronomic observatory; RQ, Barranco de la Degollada. Location coordinates for these sample sites can be seen in Table S1.

individuals was removed with tweezers, taking care not to harm the lizards. The removed shed skin was then stored in dry 1.5 mL vials and labelled accordingly for body region, individual identification and collection location. We collected from one to three samples from an individual lizard from different regions of the body. Only the skins of the non-regenerated tails were collected. The total number of skin samples used in this study was 144. The size of the lizards was measured as snout to vent length (SVL) using a straight-line ruler with an accuracy of 1 mm.

Scale morphology data collection

The skin samples were stretched over a glass slide, straightened and photographed using a digital microscope (Keyence VHX-7000). Multiple morphological measurements, including length, width and area, of individual lizard scales were obtained from the images using the image processing software ImageJ. A designated macrocode (Fig. S1) (nrttaye4033, 2023) was used to automate measurements on selected objects, reducing the potential for human error. Five individual scales were selected within each image to be measured in order to account for natural variation between scales within each body region. This was done by outlining each scale manually, using the lasso tool, which would then be automatically measured by the macro code to determine the length and width of each scale. Due to variations in image orientation, ‘length’ was determined as a maximum length measurement and ‘width’ was considered the dimension perpendicular to that. To increase the reliability of each value, each scale was measured twice per image, resulting in two replicates per scale. Subsequently, the mean values for both length and width were calculated for each scale. The mean measurements for length and width across the five selected scales were then calculated, resulting in a final single value for both length and width per image. The area was calculated by multiplying the mean values of length and width. Scale density was calculated in ImageJ by selecting a square area where the number of scales within this area could be counted and subsequently divided by the size of the area to give a total scale density per mm^2. It is important to note that this measured area was not fixed due to the variability of each image and scale type. Images with larger scales required a larger measurement area compared to smaller ones.

Environmental data

We downloaded a comprehensive human pressure index, that is, human footprint (HFP) from the Wildlife Conservation Society (Sanderson et al., 2022) to model the pressure of human influence at the sampling sites. The HFP measures the cumulative impact of direct pressures of human activities on the environment based on data from constructed, agricultural and pasture lands, as well as human population density, night-time lights, railways, roads and navigable waterways at a spatial resolution of 1 km × 1 km (Sanderson et al., 2002). HFP was extracted for the year 2020 (the most recent available dataset that is the closest to our sampling period, which was 2021 and 2023).

Macroclimatic variables were extracted using WorldClim 2.0 (Fick & Hijmans, 2017), and the initial dataset included elevation and 19 bio variables (definitions of bio variables are available in Fick & Hijmans, 2017). To prevent model overfitting and statistical and computational viability, all macroclimatic predictor variables, HFP2020 and elevation were checked for collinearity using the R package corrplot (Wei et al., 2017), and only one of the two correlated variables greater than a Pearson’s correlation coefficient threshold of 0.8 was selected (Gilbert et al., 2024) to be included in statistical analysis (see Fig. S2 for variable selection). Final variables included in statistical analysis were bio2 (the mean diurnal range of temperature), bio3 (isothermality) and bio15 (precipitation seasonality).

Microclimate values for all localities were obtained using the micro_era5 function from NichemapR (Kearney et al., 2020; Kearney & Porter, 2017). The micro_era5 function is an implementation of the NicheMapR microclimate model that integrates ERA5 (Hersbach et al., 2020) hourly weather data and the elevatr (Hollister et al., 2023) package for obtaining DEM using downscaling functions from the microclima (Maclean et al., 2018) package. The substrate was also modelled by connecting the micro_era5 model to the soilgrids database (Poggio et al., 2021). Conditions were simulated for 2 months—January and July—and 10 consecutive years (2013–2023), which captures the two extremes of the seasons (winter and summer) and for each hour of the day between 8:00 and 20:00 to capture conditions above ground when lizards are active and move around or bask. From the obtained predictions, we extracted values of TALOC—air temperature (°C) at local height, RHLOC—relative humidity (%) at local height, VLOC—wind speed (m/s) at local height, TAREF—air temperature (°C) at reference height, RH—relative humidity (%) at reference height, VREF—wind speed (m/s) at reference height, PCTWET—soil surface wetness, SOLR—solar radiation (W/m^2) (unshaded, adjusted for slope, aspect and horizon angle), and TSKYC—sky radiant temperature. Reference height was defined as 2 m and local height was defined as 2 cm, which was chosen as a biologically relevant height given the size of *G. galloti*. The simulations were run with observed cloud cover. The mean values of each month were calculated for all sites and used as microclimatic predictors. The same as for macroclimatic variables, we first checked for collinearity in all microclimatic predictor variables (Wei et al., 2017). January and July microclimatic variables exhibited high pairwise correlation (see Fig. S3); thus, we decided to include only values for July, which is the summer month and poses higher thermal and moisture pressures for active lizards. For the July microclimatic variables, only one of two correlated variables greater than a Pearson's correlation coefficient threshold of 0.8 was selected to be included in statistical analysis (Fig. S3). Final microclimatic variables included in statistical analysis were TALOC_July, VLOC_July, SOLR_July and PCTWET_July.

We placed UV data loggers (UV dosimeter badge NIWA UVB) in the field at eight sites. Due to the limited time of our field expedition and the small number of UV loggers ($N = 2$), we were only able to set up one logger at each site for 24 h and thus record a random sunny day in summer. The data were collected in the period between 28 July and 8 August 2021 (Table S2). UV data were collected every minute for 24 h. The dataset was trimmed to include only measurements between 07:30 and 20:50, which, given Tenerife's location in subtropical latitudes, corresponds to the daylight period during most of the year. In order to focus on meaningful UVI values, which should be above zero in daylight conditions, zero values were filtered out prior to calculating the mean values. Zero values accounted for <1% of all UVI values and were present in a similar proportion in all measurements. The comparison of data sets with or without zeros did not change the distribution of the mean values. A scatter plot was created using the ggplot2 package (Wickham, 2016) in R (R Core Team, 2021) to visualize individual UVI measurements at different times of day (Fig. S4). To obtain UVI values for the remaining eight sites where we did not place UV data loggers, we interpolated the data using the elevation relationship between UVI measured and elevation (Fig. S5) and using the na.approx function from the R package zoo (Zeileis & Grothendieck, 2005).

Statistical analysis

Prior to any analysis, it was necessary to account for the fact that larger lizards have larger scales. There is sexual size dimorphism in *G. galloti*, with females being smaller than males (Molina-Borja et al., 1997). Our dataset included males and females, but because we did not have samples of both sexes for each location, we could not include this factor in the analysis. We size-corrected scale measurements (length, width and area) by regressing the scale measurements against a measure of overall body size (SVL) and using the residuals of this regression as size-corrected scale measurements. Higher residual values of the scale size represent larger scales relative to the expected size for a given SVL.

All morphometric variables were first investigated using a principal component analysis (PCA) (Jolliffe, 2002). We used a biplot to visualize the relationships between the observations (PC scores) and the variables (PC loadings). Based on the cumulative variance, PC1 explained 81% of the variation and PC2 14% of the variation, with PC1 capturing scale size (PC loadings above 0.5 for scale length, width and area) and PC2 capturing scale density (loading >0.8) (Table S3). PC1 and PC2 scores were used in the subsequent analyses as response variables. Given that PCA analyses actually reflected three main body regions (dorsal, ventral and tail scales, see below), they were grouped in downstream analyses. The scores were adjusted for visual aid by adding a small constant (1) to make all PC values positive.

We used generalized linear models (GLMs) with a Gamma distribution and a log-link function (which was the most suitable one for our datasets) to analyse the relationship between adjusted PC1 and PC2 scores and environmental predictors: HFP2020, mean UV index (UVI), selected macroclimatic predictors (bio2, bio3 and bio15) and selected microclimatic predictors (TALOC_July, VLOC_July, SOLR_July and PCTWET_July) (Fox, 2016). To account for differences in sample sizes between observations, we weighted the model using sample size per site as the weighing term (Zuur et al., 2007). This ensured that observations with a larger sample size had a greater weight on parameter estimation. First, a full model was created, and multi-collinearity was tested using the variance inflation factor (VIF) (Fox & Monette, 1992). Predictors with VIF > 5 were tested with the *cor* function, and the one with lower explanatory power was removed until the reduced model contained predictors without multi-collinearity problems (all VIF < 5). We then performed a stepwise model selection to identify the most influential environmental predictors and determine the best fitting model (Table S4). We also compared the reduced model and stepwise-selected model using an analysis of deviance test and considered a more parsimonious model as the final one. Each significant predictor was plotted with data points, regression lines and the confidence intervals. All visualizations were created using the ggplot2 package in R (Wickham, 2016). All statistical analyses were performed using R (version 4.1 (R Core Team, 2021)), with the *glm* function for model fitting (R Core Team, 2021).

Results

PCA of scale morphology

From the PCA conducted on the size-corrected data, it was determined that 81% of the variance could be explained by PC1, 14% by PC2 and <5% by PC 3 and 4 (Table S3). PC1 displayed the highest positive loadings for length, width and area, indicating that the primary axis of variation in scale morphology was related to size measurements, and we refer to PC1 as 'scale size' from now on. PC2 reflected a strong positive correlation with variation in scale density; henceforth, we refer to PC2 as 'scale density' from now on. Visualizing the first two PCs as a biplot revealed three distinct scale types: dorsal, ventral and tail scales (Fig. 2). Dorsal scales exhibited negative correlations with scale size, suggesting that they are the smallest. The middle position on this axis was occupied by tail scales, suggesting that they were of middle size, and ventral scales exhibited a positive correlation, suggesting they

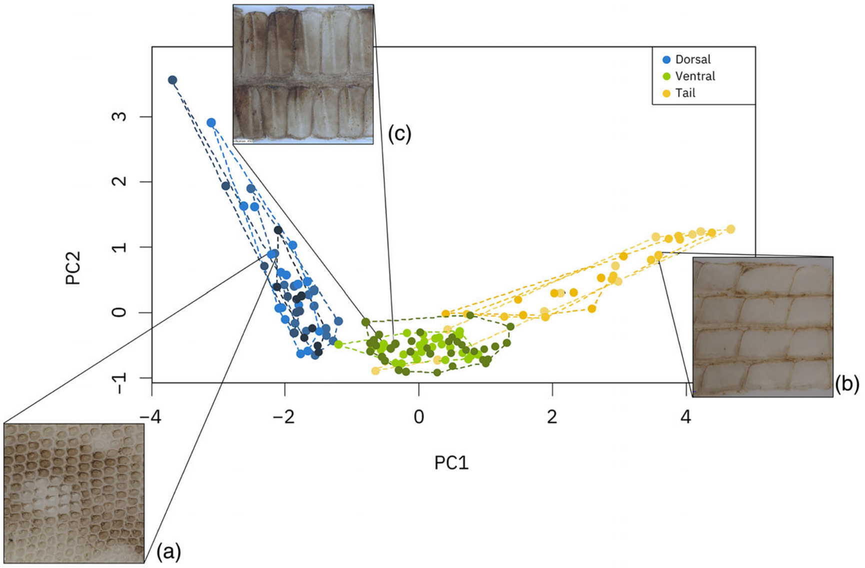

Figure 2 A biplot of the principal component analysis (PCA) for scale morphology measurements of *Gallotia galloti*. Three clear groupings of scale type can be observed. (a) Dorsal scales are characterized as being small and of variable density. (b) Ventral scales are the largest in size and of the least density. (c) Tail scales are medium size and relatively vary in density.

were the largest (Fig. 2). On the PC2 axis, we observed the least variation in scale density in the tail scales compared to the ventral and dorsal scales (Fig. 2). Dorsal scales exhibited the highest density, followed by tail scales, while the ventral scales were the least dense (Fig. 2).

Dorsal scale morphology versus environmental predictors

For dorsal scale size, the most parsimonious model included three environmental predictors: temperature, wind speed, and solar radiation (Table 1, AIC = 1461.3). Among these, solar radiation showed the strongest positive effect ($\beta = 0.004$, $P = 0.007$), indicating that greater exposure to sunlight was associated with larger dorsal scales (Fig. 3b). In contrast, wind speed ($\beta = -0.27$, $P = 0.041$) had a negative effect, suggesting that stronger winds corresponded to smaller dorsal scales (Fig. 3b). Temperature had a weak non-significant effect ($\beta = -0.02$, $P = 0.086$).

For density of dorsal scales, the most parsimonious model also included temperature, wind speed and solar radiation, as well as the human footprint index (Table 1, AIC = 777.1). Similar to scale size, solar radiation showed the strongest effect on scale density ($\beta = -0.14$, $P = 0.006$), but in an opposite direction, indicating that higher solar radiation corresponded to lower scale density (Fig. 3e). Wind speed ($\beta = 0.99$, $P = 0.031$) had a positive effect, suggesting that higher wind speed was associated with greater dorsal scale density (Fig. 3d). Temperature was at the border of significance ($\beta = 0.07$, $P = 0.057$), and there was a moderate positive relationship (Fig. 3c), suggesting that higher temperature was associated with higher dorsal scale density.

Ventral scale morphology versus environmental predictors

Of the predictors tested for correlation with ventral scale size, only human footprint index was included in the final, simplest model. Human footprint index ($\beta = 0.0002$, $P = 0.006$) had a positive effect, suggesting that higher human footprint values were associated with bigger ventral scales (Fig. 4a).

For ventral scale density, human footprint index and one climatic predictor (bio3) were included in the final, simplest model. Human footprint index ($\beta = 0.0001$, $P = 0.047$) had a moderate positive effect, suggesting that higher human footprint values were associated with greater ventral scale densities (Fig. 4b). Bio3 ($\beta = 0.03$, $P = 0.026$) also had a moderate positive effect with ventral scale density. This suggests that higher isothermality values correspond with higher ventral scale densities (Fig. 4c).

Tail scale morphology versus environmental predictors

Of the predictors tested for correlation with tail scale size, mean UVI and solar radiation were included in the final, simplest model. Solar radiation ($\beta = -0.005$, $P = 0.014$) had a negative effect, suggesting that it was associated with smaller tail scales (Fig. 5a), whereas the mean UVI ($\beta = 0.08$, $P = 0.150$) was not significant.

For tail scale density, besides UVI and solar radiation, three other climatic predictors were included in the final most simple model: bio2, bio15 and wind speed. Only wind speed ($\beta = 0.39$, $P = 0.070$) was close to significant, and it showed a moderate positive effect, suggesting that higher wind speed was associated with greater tail scale densities (Fig. 5b).

Table 1 Summary results of the most parsimonious generalized linear model of scale size (PC1) and scale density (PC2) tested with environmental predictors

Morphology trait	Body part	Predictor	Estimate	SE	*t* Value	*P*-value	d.f.	R^2	AIC
Scale size	Dorsal	Intercept	−0.68	0.72	−0.94	0.355	47	0.14	1461.26
		TALOC_July	−0.02	0.01	−1.75	0.086			
		SOLR_July	**0.004**	**0.001**	**2.83**	**0.007**			
		VLOC_July	**−0.27**	**0.13**	**−2.11**	**0.041**			
Scale density	Dorsal	**Intercept**	**5.38**	**2.54**	**2.11**	**0.040**	47	0.80	777.12
		HFP2020	−0.0001	0.0001	−1.08	0.289			
		TALOC_July	**0.07**	**0.03**	**1.96**	**0.057**			
		VLOC_July	**0.99**	**0.44**	**2.22**	**0.031**			
		SOLR_July	**−0.01**	**0.01**	**−2.91**	**0.006**			
Scale size	Ventral	Intercept	0.22	0.22	1.00	0.327	31	0.31	1092.31
		HFP2020	**0.0002**	**0.0001**	**2.98**	**0.006**			
Scale density	Ventral	**Intercept**	**−1.32**	**0.51**	**−2.59**	**0.015**	31	0.40	673.94
		HFP2020	**0.0001**	**0.0001**	**2.08**	**0.047**			
		bio3	**0.03**	**0.01**	**2.34**	**0.026**			
Scale size	Tail	**Intercept**	**2.41**	**1.04**	**2.32**	**0.024**	63	0.26	1526.36
		mean_UVI	0.08	0.05	1.46	0.150			
		SOLR_July	**−0.01**	**0.002**	**−2.52**	**0.014**			
Scale density	Tail	Intercept	−0.37	1.45	−0.26	0.798	63	0.15	185.44
		mean_UVI	−0.06	0.07	−0.87	0.387			
		bio2	0.12	0.07	1.63	0.110			
		bio15	0.02	0.02	0.87	0.386			
		VLOC_July	**0.39**	**0.21**	**1.85**	**0.070**			
		SOLR_July	−0.01	0.00	−1.55	0.127			

Estimates, standard error (SE) *t*- and *P*-value are presented. Statistically significant predictors of <0.05 are shown in bold. Nagelkerke's R^2 values were calculated, and AIC values of the model are presented.

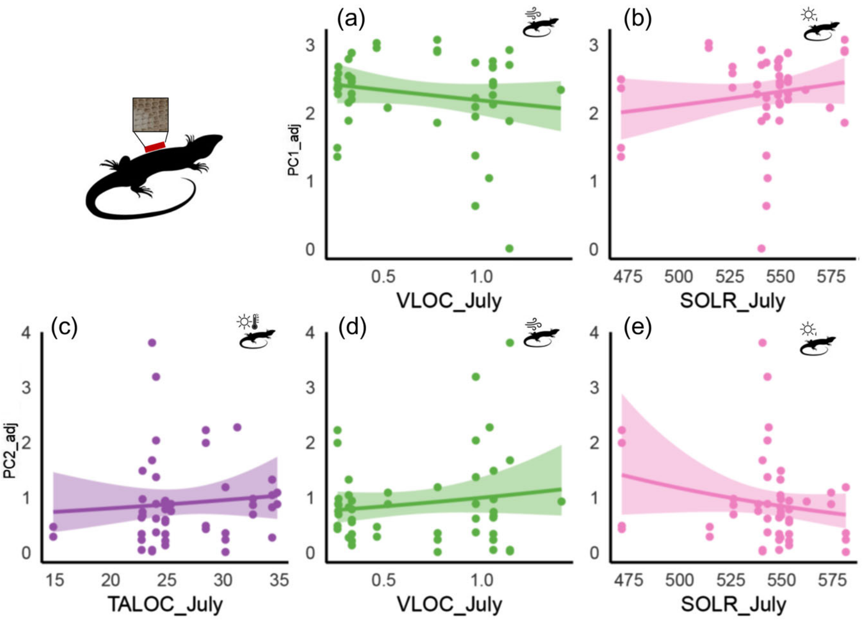

Figure 3 Dorsal scale size of *Gallotia galloti* under different environmental factors. Relationship between dorsal scale size (captured in adjusted PC1 values) (a, b) and scale density (captured in adjusted PC2 values) (c–e) and significant environmental predictors. Linear regression lines and 95% confidence intervals are indicated for each body part.

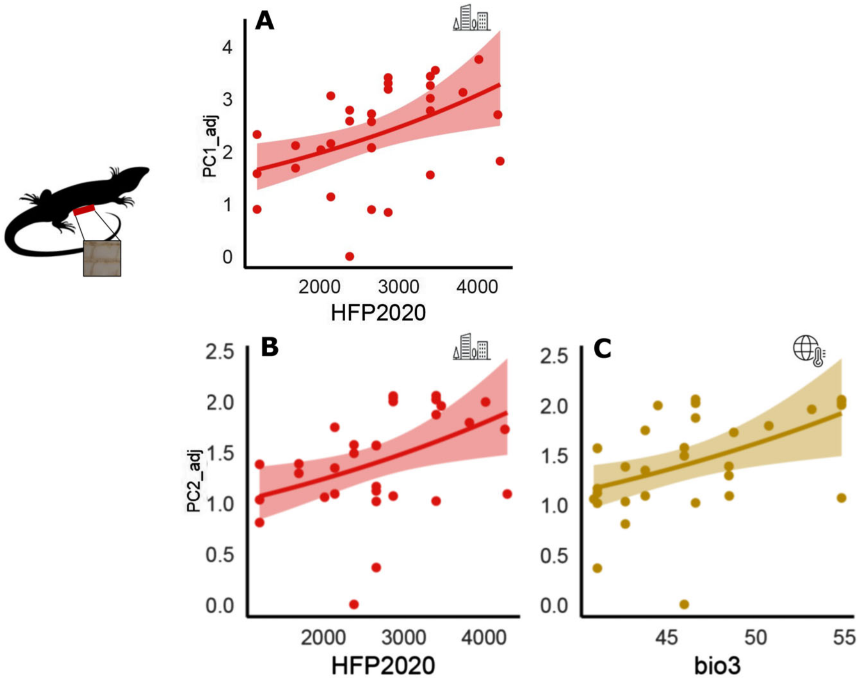

Figure 4 Ventral scale size of *Gallotia galloti* under different environmental factors. Relationship between ventral scale size (captured in adjusted PC1 values) (a) and scale density (captured in adjusted PC2 values) (b, c) and significant environmental predictors. Linear regression lines and 95% confidence intervals are indicated for each body part.

Discussion

In our study, we explored intraspecific scale ecomorphology across a broad range of environmental variability in a lizard. Our results provide insights into how environmental factors influence the scale morphology in *Gallotia galloti* across 3700 m of elevation and a wide climatic gradient, considering both long-term macroclimatic conditions and short-term microclimatic conditions, as well as different levels of anthropogenic influence. To our knowledge, this is the first such study where interspecific variation in scale morphology is studied over a large elevation and climatic gradient.

First, PCA results showed that the primary axis of variation in scale morphology was strongly associated with scale size (PC1 explained 81% of the total variance), suggesting that size differences among scales are the dominant morphological trait, which is consistent with findings in other reptilian taxa where scale dimensions are a primary driver of variation (Rutland et al., 2019). Notably, three distinct scale sizes were identified: dorsal, ventral and tail scales, each occupying separate regions of morphospace and differing most clearly on the first PCA axis. This clear distinction in the size of scales across body regions suggests that they may have evolved to fulfill different functional roles in response to different environmental pressures such as thermoregulation, water retention or mechanical protection (Oufiero et al., 2011; Wegener et al., 2014). The second axis of variation from the PCA results was strongly associated with scale density but explained only a smaller fraction of total variance (14%). Scale density is, however, an important morphological trait because it indicates how tightly or loosely packed together the scales are, which may play a role in retaining water during dry conditions. We further investigated in our study how different environmental predictors correlate with scale size and density as captured in PC1 and PC2.

On the long-term macroclimatic scale, only the bioclimatic variable (Fick & Hijmans, 2017) related to temperature stability significantly influenced the scale morphology of *G. galloti*. Isothermality (Bio3) was associated with variations in ventral scale density, suggesting that the relationship between diurnal and annual variation in temperature may exert selective pressures on the ventral part of the integument of this species. Higher isothermality was associated with higher ventral scale density, suggesting that having denser scales in sites with higher day-to-night (diurnal) temperature variation, which is relatively large compared to seasonal (annual) variation, might be beneficial. Furthermore, we modelled microclimatic temperature conditions in July at a height of 2 cm above the ground as experienced by the lizards and only for the daytime hours when lizards are active. We observed significant correlations between temperature at 2 cm above ground and dorsal scale density. Higher temperatures were strongly associated with higher dorsal scale density. This finding supports our initial prediction that scale morphology responds to temperature gradients and is in line with some previous studies (Oufiero et al., 2011; Soulé & Kerfoot, 1972). It likely reflects a

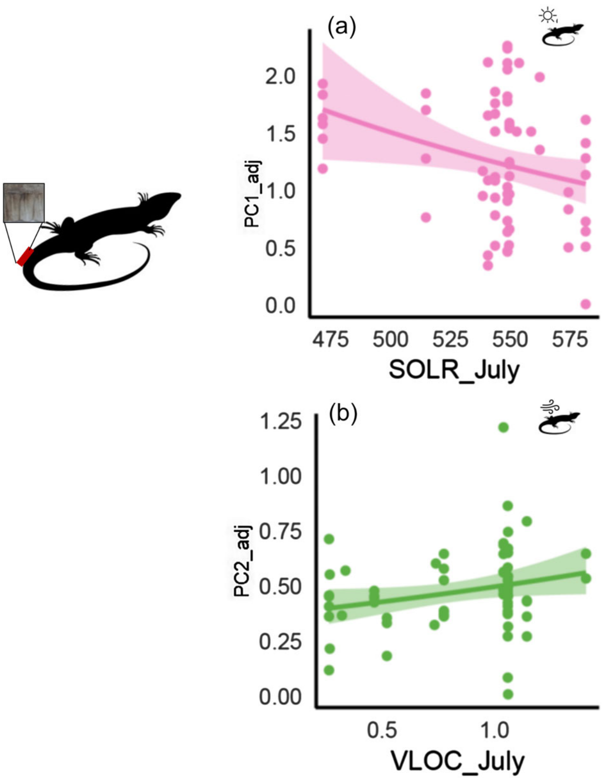

Figure 5 Tail scale size of *Gallotia galloti* under different environmental factors. Relationship between ventral scale size (captured in adjusted PC1 values) (a) and scale density (captured in adjusted PC2 values) (b) and significant environmental predictors. Linear regression lines and 95% confidence intervals are indicated for each body part.

thermoregulatory adaptation in which denser scales reduce heat uptake and improve heat dissipation in hotter microclimates (Oufiero et al., 2011).

We also explored the relationship between solar radiation and scale morphology. Higher solar radiation was associated with larger scales and lower scale density in the dorsal region and smaller scales in the tail region of the body. This could indicate a potential photoprotective function, where larger dorsal scale size, which is exposed to the sun, may help to mitigate UV-induced damage, particularly in populations at elevations above 2000 m a.s.l., where UV radiation is most intense (Reguera et al., 2014). These findings align with previous research demonstrating that UV exposure is an important determinant of scale morphology in reptiles (Gómez-Benitez et al., 2021). Furthermore, it aligns with our second hypothesis that increased UV radiation exerts selective pressure on dorsal scale morphology, which has also been suggested for skin morphology variation in Iguanians (Tulli & Cruz, 2018). However, contrary to our expectations, no direct relationship was found between UVI and scale size or density in the dorsal scales (mean UVI was excluded from the simplest models). The solar radiation predictor that we used may be more complex and include other functionally relevant environmental stresses, including UV radiation, and therefore showed a response in our data, whereas mean values of UVI alone did not. Moreover, photoprotective adaptations are complex and may occur at other levels, such as pigmentation, physiological or behavioural strategies (Clusella-Trullas et al., 2009; Conley & Lattanzio, 2022; Gilbert et al., 2024; Reguera et al., 2014), reducing pressure for morphological changes in scales.

Our results further suggest that the morphology of scales plays a role in hydroregulation. Wind speed significantly influenced the size and density of the dorsal scales and the density of tail scales, which are the ones exposed to the wind in a lizard. In dorsal scales, increased wind speed was associated with smaller but denser scales, suggesting a possible protective adaptation against desiccation with more tightly packed scales under stronger wind exposure in the environment. Conversely, for tail scales, higher wind speeds were linked to lower density of scales, which could suggest that the tail is not playing a major role in hydroregulation compared to the dorsal side of the body. Finding smaller scales in more windy places that likely exert higher water loss pressures was not in line with our hypothesis and is opposite to some previous studies that suggest that in dry and hot environments, large scales reduce water loss through evaporation (Alibardi, 2003; Dmi'el, 2001; Sinervo et al., 2010; Wegener et al., 2014), mainly because large scales per unit of skin surface offer fewer imbrications. But on the other hand, we observed that hotter and more windy places both correlated with higher density of dorsal scales in *G. galloti*, thus, with spaces between scales more tightly packed to prevent water loss, which is in line with the suggestion that the spaces between scales may have higher permeability for water (Calsbeek et al., 2006).

The morphology of the ventral scales also varied with the Human Footprint Index (HFP2020), indicating possible responses to habitat degradation. The size and density of ventral scales increased with higher HFP values. This pattern may reflect an adaptive response to altered microhabitat conditions in urban areas and is consistent with previous studies that have shown that reptiles in human-altered environments exhibit morphological changes in response to altered microhabitats and resource availability (Gómez-Benitez et al., 2021). However, further and more detailed studies would need to be conducted to decipher the effects of various human activities on the life-history traits of lizards, which may be related to their scale morphology. Human settlements and other anthropogenic activities are most pronounced in the coastal areas of Tenerife, while the extreme high elevations are almost free of human disturbance. It could be that the relationship between scale morphology and HFP2020 is a derivative of the inverse relationship with elevation and associated climatic conditions (the correlation between elevation and HFP was close to 0.7), but this would also need further investigation.

Overall, our findings contribute to the growing body of research on reptilian scale morphology and its environmental determinants. The observed patterns indicate that *G. galloti* exhibits morphological variability in response to temperature seasonality, local temperature and wind conditions, solar radiation and human pressure. These adaptations likely play a crucial role in thermoregulation, photoprotection and water balance of *G. galloti*. Future research should further explore the genetic basis of this morphological variation and assess how ongoing climate change may shape scale morphology in lizard populations across diverse habitats, or *vice versa*, how scale morphology may affect species distribution.

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AŽ and MP conceived the ideas and designed the methodology; AŽ, RMP, SBC, UD and MP collected the data; KK, MP, UD and AŽ analysed the data; AŽ and KK led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Location names, ID, coordinates and elevation data for the sample sites of *Gallotia galloti* in Tenerife.

Table S2. Details of measurements obtained with UV data logger for eight sites.

Table S3. Principal component analysis (PCA) of scale morphology variables in *Gallotia galloti*.

Table S4. Full GLM model built (top row) and predictor reduction process with analysis of deviance results of comparison between the reduced and the stepwise-selected model for each dataset (dorsal, ventral and tail scales vs. PC1 and PC2).

Figure S1. ImageJ macro code used to automatically run length and width measurements of a selected area.

Figure S2. Collinearity plot with elevation and all macro climatic predictors and elevation tested for collinearity.

Figure S3. Collinearity plot with all micro climatic predictors tested for collinearity.

Figure S4. Plotted daily UVI measurements collected with UV data logger for one day at eight different sites.

Figure S5. Mean measured UV index (UVI) at 8 sites over the entire altitude range and interpolated UVI values of the remaining 8 sites.