

TITLE

Sex-specific responses of phenotypic diversity to environmental variation

AUTHORS

Adam C. Algar (Corresponding Author)

School of Geography, University of Nottingham, Nottingham NG7 2RD UK

adam.algar@nottingham.ac.uk

Marta López-Darias

Island and Evolutionary Research Group, Instituto de Productos Naturales y Agrobiología, IPNA-

CSIC, Tenerife, Canary Islands, Spain;

mdarias@ull.es

KEYWORDS

Convex hull, ecological radiation, ecomorphology, elevation gradients, environmental filtering, intraspecific variation, lizards, sexual selection, sexual size dimorphism, trait dispersion

ABSTRACT

Identifying the factors generating ecomorphological diversity within species can provide a window into the nascent stages of ecological radiation. Sexual dimorphism is an obvious axis of intraspecific morphological diversity that could affect how environmental variation leads to ecological divergence among populations. In this paper we test for sex-specific responses in how environmental variation generates phenotypic diversity within species, using the generalist lizard *Gallotia galloti* on Tenerife (Canary Islands). We evaluate two hypotheses: the first proposes that different environments have different phenotypic optima, leading to shifts in the positions of populations in morphospace between environments; the second predicts that the strength of trait-filtering differs between environments, predicting changes in the volume of morphospace occupied by populations in different environments. We found that intraspecific morphological diversity, provided it is adaptive, arises from both shifts in populations' position in morphospace and differences in the strength of environmental filtering among environments, especially at high elevations. However, effects were found only in males; morphological diversity of females responded little to environmental variation. These results within *G. galloti* suggest natural selection is not the sole source of phenotypic diversity across environments, but rather that variation in the strength of, or response to, sexual selection may play an important role in generating morphological diversity in environmentally diverse settings. More generally, disparities in trait-environment relationships among males and females also suggest that ignoring sex differences in studies of trait dispersion and clustering may produce misleading inferences.

INTRODUCTION

Evolutionary radiation can generate exceptional ecological diversity among species; however not all clades radiate ecologically (Schluter 2000, Losos and Mahler 2010, Blankers et al. 2012).

Environmental features can both encourage evolutionary radiation, via ecological opportunity (Schluter 2000), or inhibit it, e.g. through insufficient area or heterogeneity (Ricklefs and Lovette 1999, Losos and Schluter 2000, Algaer and Mahler 2015). Understanding how, and when, environmental variation influences ecological diversification is thus a key question for evolutionary biologists and ecologists (Blankers et al. 2012, Kaliontzopoulou et al. 2014).

The relationship between a species' environment and its morphological variability has received substantial attention in a wide variety of lizard groups. For example, limb length is known to be adaptive for improved locomotion on particular substrates, such as narrow versus broad perches (*Anolis*; Losos et al. 2000), open *versus* closed habitats (*Niveoscincus*; Melville and Swain 2000) or terrestrial versus arboreal habitats (chameleons; Bickel and Losos 2002). Other traits, such as head characteristics (Huyghe et al. 2007, Measey et al. 2009) and colour pattern (Forsman and Shine 1995) are also known to differ among environments in lizards. At broader scales, body size shows considerable variability along elevation and latitudinal clines (Ashton and Feldman 2003, Pincheira-Donoso et al. 2008, Muñoz et al. 2014a). Other traits, such as physiological tolerance, visual system, and behavior also vary with environmental conditions in lizards (Leal and Fleishman 2002, Ord et al. 2010, Johnson et al. 2010, Muñoz et al. 2014b).

Studies of morphological variation within clades and communities have traditionally focused on mean differences among species, and thus attempt to reconstruct the drivers of ecological diversification after the fact. An alternative approach is to examine how morphological variation is generated among populations that have not (yet) undergone speciation, providing insight into the nascent stages of ecological diversification and adaptive radiation (Thorpe and Baez 1987, Thorpe et al. 2010). More generally, identifying the factors driving intraspecific morphological variation can also provide

insight into the factors driving ecological function and dynamics within communities (Bolnick et al. 2011, Violle et al. 2012).

As populations diversify, they can fill ecological space in new ways. Specifically, environments may differ in their ecological optima, leading to directional selection and shifts in a population's position within ecological space. For example, Caribbean *Anolis* lizards have repeatedly evolved toward different phenotypic optima depending on their microhabitat use (Mahler et al. 2013). Environments may also differ in the range of ecological variation they can support, i.e. in the strength of the environmental filter they impose (Weiher et al. 1998, Cornwell et al. 2006, Violle et al. 2012), constraining the volume of ecological space occupied by a species, or population (Weiher et al. 1998, Cornwell et al. 2006, Algar et al. 2011, Violle et al. 2012). These two options are not mutually exclusive and could act in concert or opposition to influence how populations fill ecological space across heterogeneous environments.

Sexual dimorphism is a fundamental axis of morphological variation in animals (e.g. Fairbairn et al. 2007) and may contribute substantially to ecological and lineage diversification in a number of ways. Sexual selection, which can produce sexual size dimorphism via male-male competition or fecundity selection in females (Cox et al. 2003), has been identified as a driver of speciation (Panhuis et al. 2001, Hudson and Price 2014). However, sexual dimorphism may also inhibit diversification if males and females of dimorphic species use a wide range of resources (Bolnick and Doebeli 2003, Ritchie 2007). Sexual dimorphism may also reflect both natural and sexual selection: Lopez-Darias et al. (2014) showed, in *Gallotia* lizards in the Canary Islands, that the same traits (head size and bite force) may be under sexual selection for one sex (males) and natural selection for the other (females). Regardless of whether dimorphism arose from sexual or natural selection, morphological differences between males and females can translate into ecological differences (Schoener 1967, Shine 1989, Butler et al. 2000, Butler and Losos 2002, Bolnick et al. 2011), raising the possibility that males and females may respond differentially to environmental variation. For example, Butler & Losos (2002) found that *Anolis* ecomorphs in different microhabitats also varied in their degree of sexual

dimorphism. Similarly, habitat \times sexual dimorphism interactions have been identified within lacertid lizards, where populations diverge sexually to varying extents in traits, like limb length, related to habitat use (Kaliontzopoulou et al. 2010). The degree of sexual size dimorphism can also vary across broad scale climatic gradients (Fitch 1981, Stillwell and Fox 2009, Laiolo et al. 2013), though such patterns are variable across taxa (Blanckenhorn et al. 2006). Rensch's rule states that sexual size dimorphism increases with body size; in species with larger males, this is due to greater variation in males than females (Abouheif and Fairbairn 1997). Though Rensch's Rule applies inconsistently within species (Blanckenhorn et al. 2006), it suggests that, in species with larger males, differences in sexual dimorphism among environments will arise from variation in males, rather than females.

In this paper we test whether differences in how populations fill morphological space (morphospace) in different environments arise from differences in the phenotypic optima among environments (optimum-shift hypothesis), or in the strength of environmental filtering (environmental filter-strength hypothesis), or a combination of both. The optimum-shift hypothesis predicts that a population's centroid in morphospace will be further from the species' (all populations pooled) centroid than expected based on a null model of randomly assembled populations. The environmental filter-strength hypothesis predicts that the volume of morphospace occupied by a population (i.e. its convex hull; Cornwell et al. 2006) will be smaller than predicted based on the same null model, i.e. traits will be clustered. We also evaluate whether the response of morphospace filling to environmental variation differs between males and females. We test these hypotheses for *Gallotia galloti*, a widespread, generalist lizard on the environmentally diverse island of Tenerife (Canary Islands).

METHODS

Study system

Tenerife, the largest island in the Canary Islands is environmentally very diverse. Covering over 2,000 km² and rising to more than 3,700 m above sea level, it hosts a wide range of habitats, including sub-desert coastal scrub, thermophilous, pine and laurel forest, and high elevation scrub/alpine ecosystems (Fernández-Palacios and Whittaker 2008, Zobel et al. 2011). These habitats arise in large

part from the influence of elevation and orientation with respect to the humid northeast trade winds (Fernández-Palacios and Nicolás 1995, Fernández-Palacios and Whittaker 2008). Although human habitat modification, primarily through agriculture and tourism-related development, has greatly reduced the extent of most natural habitats, it has also generated agricultural and urban habitats at the regional scale (Fernández-Palacios and Whittaker 2008).

Although Tenerife (and the Canaries more generally) harbours several stunning evolutionary radiations, especially of plants and arthropods (e.g. Arnedo et al. 2001, Arechavaleta et al. 2009, Vitales et al. 2014), the lizard fauna has not radiated extensively within islands (Cox et al. 2010). Just four native lizard species inhabit Tenerife: one endemic gecko, one endemic skink, and two extant lacertid species of the endemic Canarian genus, *Gallotia*. Of these, *G. galloti* is by far the most widespread and abundant. Its only extant putative lizard competitor, *G. intermedia*, is extremely geographically restricted, limited to a small area of cliff habitat. Thus, despite Tenerife's substantial environmental diversity, its herpetofauna is dominated by a single, widespread species.

G. galloti is a medium sized, omnivorous lizard (Fig. 1), restricted to Tenerife and La Palma and is one of the dominant and most conspicuous native vertebrates on both islands. *G. galloti*'s ancestor likely colonized Tenerife's proto-islands 9-10 mya (Cox et al. 2010) and it currently occupies every major habitat and geographical region in Tenerife, though its abundance in the northern tip of the island, Anaga, seems to be markedly lower than elsewhere (Thorpe and Baez 1987). It and its congeners are sexually dimorphic, especially in body size (males are larger), but also, for most species, in body shape, limb length and head size (Thorpe and Baez 1987, Molina-Borja et al. 1997, 2010, Herrel et al. 1999, Molina-Borja 2003, Lopez-Darias et al. 2014).

In addition to substantial sexual dimorphism, *G. galloti* also exhibits extensive morphological variation through space. Thorpe and Baez (1987) surveyed 18 populations of *G. galloti* across Tenerife and identified considerable geographical variation in body and head size, scalation and colour. However, geographical concordance across sexes and traits varied considerably. For example,

body size showed very different patterns in males and females, while head size varied similarly between sexes (though males had larger heads). Traditionally, phenotypic differences have led to the delineation of two subspecies (or races) on the island (*G. galloti galloti* and *G. galloti eisentrauti*) that differ in colouration (Thorpe and Baez 1987, Molina-Borja et al. 1997). *Gallotia g. eisentrauti* also tends to be larger (Molina-Borja et al. 1997), though this difference is less clear when variation in *G. g. gallotia* due to contact zones and elevation is incorporated in the comparison (Thorpe and Baez 1987).

Quantifying environmental variation

We identified areas of similar environmental conditions on Tenerife, following the approach used by Hortal and Lobo (2005) and Hortal et al. (2007). Firstly, because climatic variables tend to be correlated through space, we performed a principal component analysis on climate and topographic variables sampled at a 500m resolution across. We included the following variables: elevation, aspect, and mean annual, maximum and minimum temperature and annual, monthly minimum and maximum precipitation (Fig. A1; raw data from Hortal et al. (2006), shared by J.M. Lobo). For aspect, we computed ‘northness’ [northness = cosine(aspect)] and ‘eastness’ [eastness = sine(aspect)], where aspect is measured in radians. We extracted the first three principal components for the subsequent clustering analysis. Environmental PCs 1-3 accounted for 88% of the total variance (Table A1) and co-varied with temperature and elevation (envPC1), aridity and northness (envPC2) and eastness (envPC3), respectively. These captured the three major axes of environmental and ecosystem variation on Tenerife (Fig. A2).

We used k-means clustering of environmental PCs 1-3 to delineate environmental zones on Tenerife. We used $k = 4$ as this captured 70% of the environmental variation on Tenerife with a tractable number of environmental zones to encompass variation in our model organism (Fig. 2). Environment A is found at low southern elevations characterized by high temperatures and low rainfall. Environment B is found at mid elevations, with southern exposure, cooler temperatures and more rainfall than Environment A. Environment C represents the north of the island at low to mid

elevations, and has northerly slopes with much higher rainfall and humidity due to the influence of the trade-winds. Environment D is found at the highest elevations on the Teide volcano, and is characterized by extreme temperatures, especially cold, and widely seasonal precipitation patterns (including snow).

Lizard sampling

We sampled lizards in August 2011 at 20 sites across Tenerife. Sites were representative of the major environmental zones (Fig. 2). At each location, we trapped lizards for one to four consecutive days using pitfall traps baited with tomato or banana. After we measured them, lizards were released precisely where they were caught. Captured lizards were temporarily marked with a marker pen on the abdomen to avoid re-measuring the same individual. At each site, we aimed to trap 10-12 lizards of each sex (identified by appearance and/or evert ing hemipenes or checking the abdomen for eggs). Individuals that could not be reliably sexed (e.g. females versus juvenile males) were excluded. At some sites, the target sample size could not be obtained, while at others, high abundance meant more lizards could be measured (Table A2).

Quantifying morphological variation

We measured 14 traits relating to body size (snout-vent length; SVL), leg and toe length, and head length, height and width (Table 1; Fig. A3). MLD performed all measurements to eliminate measurer effects. To account for the effect of body size, we regressed the logarithm of each trait on log SVL and used the residuals in subsequent analyses (e.g. Pinto et al. 2008). Next, we identified key axes of morphological variation using a principal component analysis on these residuals (Table A3). We retained the first three principal components, which accounted for 73% of the total variance (Table A3; PC1 = 54.3%, PC2= 11.4%, PC3=7.2%). We used a varimax rotation to clarify the loading structure and increase interpretability. After rotation, PCs 1-3 loaded heavily on head size, toe length, and leg length, respectively (Table 1).

Testing for trait and sexual dimorphism variation across environments

We used linear mixed models to test for differences in trait means and sexual dimorphism across environments. For each trait (SVL; head size: PC1; toe length: PC2; and leg length: PC3), we first tested for variation in sexual dimorphism across environments using a model with a sex-environment interaction. We included environment and sex, and their interaction, as fixed effects and site as a random effect using the nlme package (Pinheiro et al. 2014) in R. If the environment by sex interaction was not significant ($\alpha = 0.05$, Wald's test), we removed it from the model. We compared models assuming equal variances with models that accounted for differing variances among environments using AIC_c.

Testing the optimum-shift and environmental filter-strength hypotheses

We used three morphological axes for the morphospace analysis: SVL (log-transformed), head size (PC1), and leg length (PC3). We omitted toe length (PC2) because we found no differences between environments or sexes in this trait (Table 2). We standardized each trait (logSVL, PC1 and PC3) to have a zero mean and unit variance before computing convex hulls. Estimates of convex hull volume are sensitive to sample size; larger samples are more likely to contain extreme values. To account for unequal sampling across environments, we randomly subsampled 20 males and 20 females from each environment and used these subsets to compute convex hull volumes. We repeated this sub-sampling 100 times and used the mean in subsequent analyses.

We measured the volume of morphospace occupied by lizards from each environment and all environments together using convex hull analysis (Cornwell et al. 2006), where morphospace was defined by three axes: body size, head size and limb length. Our measure of volume is equivalent to the functional richness of a species assemblage (Villéger et al. 2008). Next, we measured the morphological dissimilarity of lizard populations among the four environments, following Villéger et al (2011). The morphological dissimilarity is the percentage of morphospace volume that is occupied uniquely by, in this case, lizards from a single environment. We computed the total morphological dissimilarity among all environments, as well as all six pairwise combinations. We used the 'hypervolume' package (Blonder et al. 2014; Blonder 2015) in R v.3.2.1 (R Core Team 2015) to

compute convex hulls for each environment and their unions. We repeated this analysis for each trait individually, using trait ranges instead of convex hulls. All analyses were carried out with both sexes pooled and for males and females separately.

To test the environmental filter-strength hypotheses, we compared the convex hull volume for lizards from each environment to the volume expected from a null model. For the optimum-shift hypothesis, we calculated the distance from each population's morphospace centroid to the centroid of all populations pooled and compared this to a null expectation. The null expectation was created for each environment by randomly selecting 40 individuals (20 males and 20 females) without replacement from the entire pool of individuals. We repeated this 1000 times to compute P-values and their 95% confidence intervals following Ruxton and Neuhauser (2013), with the observed value included in both the numerator and denominator of P-value calculations. All tests were two-tailed.

RESULTS

Testing for trait and sexual dimorphism variation across environments

We found considerable sexual size dimorphism in *Gallotia galloti*, with males achieving much greater SVL than females (Figs. 3 and 4). However, we also found a significant interaction between sex and environment in our linear mixed effects model (Table 2; $F_{3,328} = 7.69$, $P < 0.001$) indicating that the degree of sexual size dimorphism varied among environments. No other traits showed a significant sex \times environment interaction (Table 2). Models assuming equal variances among environments had lower AIC_c values than models that allowed variances to vary for all traits except head size (PC1 $\Delta AIC_c = 5.6$). Thus for this trait, we present results from models allowing unequal variances among environments. Results were nearly identical (and there were no changes in significance) regardless of which models were used.

Once the sex \times environment interaction was removed, we found significant sexual dimorphism in head size (PC1) and leg length (PC3), but not toe length (PC2; Table 2). Males tended to have larger heads and longer legs, relative to body size, than females. Head size (PC1) and leg length (PC3) also

varied across environments, independently of sex, ($P \leq 0.02$ for both; Table 2). The trend was for greater relative male head size and longer relative leg lengths at high elevations (Environment D; Fig. 3).

Environmental variation and morphological dissimilarity

Morphological dissimilarity, i.e. the percentage of morphospace uniquely occupied by lizards from a single environment, was 36% (Fig. 5), but this was not significant based on our null model ($P = 0.15$, $CI_{95} = 0.13\text{--}0.18$). Individual contributions of environments to this value ranged from 3% to 17% (Table A4), but only Environment C's unique volume differed significantly from the null expectation, though the 95% confidence interval still overlapped 0.05 ($P = 0.041$, $CI_{95} = 0.029\text{--}0.053$). Pairwise dissimilarity (i.e. morphological turnover) among environments ranged from 51% – 74%, but only comparisons involving the high elevation Environment D were significant (Table A5).

Partitioning the data by sex revealed different patterns among males and females. Males underwent more morphological turnover between environments than females (61% versus 42%). Moreover, for males, this morphological turnover was significant ($P = 0.023$, $CI_{95} = 0.014\text{--}0.032$) while for females it was not ($P = 0.43$, $CI_{95} = 0.39\text{--}0.45$). However, uniquely occupied volumes were not significant for any environment for either males or females, though P-values were low for Environment C (Table A4), suggesting no single environment drives morphological dissimilarity. Pairwise morphological dissimilarity for males was higher than for females. For the former, all environments differed significantly from Environment D, while for females only Environments B (mid elevation) and D (high elevation) differed significantly (Table A5).

Individual trait dissimilarity among environments

When sexes were pooled, individual trait dissimilarity was 20% for body size (log SVL), 14% for head size (PC1) and 11% for leg length (PC3), though only body size dissimilarity was significant ($P = 0.004$, $CI_{95} = 0.000088\text{--}0.0008$). Males and females both showed greater dissimilarity for body size

than other traits, with males having greater dissimilarity than females for all traits. However, only male body size dissimilarity was significant (Table A6; $P = 0.002$, $CI_{95} = 0.001\text{--}0.0048$).

With sexes pooled, the only significant pairwise comparisons were for body size turnover between environments B versus D, C versus D, and B versus C (Table A7). However, for males, several significant pairwise differences were found for both body size (Table A7; B versus D, and C versus D) and head size (Table 6; Environment D differed from all others). For females, body size turnover was not significant and only a single comparison was significant for leg length (Table A7; Environment B versus D).

Testing the environmental filter-strength and optimum-shift hypotheses.

When both sexes were considered together, populations at mid and high elevations (Environments B and D in Fig. 2) occupied less morphospace than lower elevation environments (Fig. 5). This clustering was strongest and significant at the highest elevations (Environment D; $P = 0.011$, $CI_{95} = 0.0045\text{--}0.017$), but weak at mid elevations (Environment B; Fig. 5; $P = 0.058$, $CI_{95} = 0.043\text{--}0.072$). Neither the low elevation northern or southern environments (Environments A and C) displayed significant clustering ($P > 0.75$ for both). Males occupied significantly less morphospace, i.e. were more clustered, at high elevations (Environment D) than expected due to chance (Fig. 5; $P = 0.033$, $CI_{95} = 0.022\text{--}0.044$), but were not clustered in any other environment ($P > 0.30$ in all cases). Although patterns of females appeared qualitatively similar to those of males, they exhibited less variation and displayed no significant clustering in any environment (Fig. 5; $P > 0.12$ in all environments).

Pooling both sexes, the mid and high elevation environments (B and D, respectively) showed greater centroid displacement than the two low elevation environments. Of the former set, Environment D was more severely displaced (Fig 5; $P = 0.001$, $CI_{95} = 0.001\text{--}0.0029$) relative to the null expectation than the lower elevation Environment B (Fig. 5; $P = 0.006$, $CI_{95} = 0.0012\text{--}0.011$). Once again, the strong departure of the high elevation Environment D was driven by male variation (Fig. 5). Males from Environment D were much further from the pooled morphospace centroid than expected from

our null model ($P = 0.002$, $CI_{95} = 0.001\text{--}0.0048$). Females show no such displacement at the highest elevations, but did for the mid-elevation Environment B (Fig. 5; $P = 0.002$, $CI_{95} = 0.001\text{--}0.0048$)

DISCUSSION

Identifying how environmental factors generate ecomorphological variation within species provides a window into the nascent stages of ecological radiation. On Tenerife, just over one third of the morphospace occupied by the lizard *Gallotia galloti* (Lacertidae) was uniquely occupied by lizards from a single environment, indicating that environmental differences are accompanied by morphological turnover (*sensu* Villéger et al. 2011) among populations. We tested two pathways by which environmental variation may have generated these differences between populations within a species, and thus enhance morphological diversity. The optimum-shift hypothesis proposes that the phenotypic optimum differs between environments, leading to divergence in ecomorphological traits between populations in different environments (Mahler et al. 2013). The environmental filter-strength hypothesis suggests that the strength of environmental filtering varies across environments, leading to differential trait-clustering (Weiher et al. 1998, Algar et al. 2011, Swenson et al. 2012). Thus, under an optimum-shift model, environment-specific selection pressures act primarily on phenotypic position in morphospace, while under an environmental filter-strength model, they act primarily on phenotypic variance.

We found that populations' morphospace volumes and centroid displacements (the distance of a population's centroid in morphospace from the overall centroid) varied among environments, and that this variation was elevationally structured. At low elevations (Environments A and C in Figure 3), neither morphospace volume nor centroid displacement differed from that expected based on random sampling from the total population. However, at mid to high elevations (Environments B and D), populations' morphospace volumes were less and centroid displacements were greater than the null expectation, suggesting an increase in trait clustering at high elevations and a shift in trait optimums.

However, the intraspecific morphological diversity observed in *G. galloti* across environments arose from environmentally structured morphological variation in males, but not in females. Variation in male lizards across environments primarily occurred along the body size axis, with weak variation in leg length and head size. Males tended to be smaller at high elevation, a common, but not ubiquitous, pattern within lizards (Ashton and Feldman 2003, Pincheira-Donoso and Meiri 2013, Muñoz et al. 2014a). In contrast, we found that female patterns of morphospace occupation did not differ from random expectations, with the single exception of centroid displacement in Environment B. Thorpe and Baez (1987) suggested that geographical patterns of male and female body size on Tenerife were incongruent. Our findings suggest that these differences—and concomitant changes in sexual dimorphism—arise, at least in part, from reduced morphological differentiation of females among environments, compared to males. This pattern is consistent with the phenomenological Rensch's rule, which suggests greater size variation among males than females (Blanckenhorn et al. 2006).

Although our results are consistent with both the optimum-shift and environmental-filter strength hypotheses, the discrepancy between male and female variation reveals a more complex story. The larger shifts in morphospace position of *G. galloti* males, relative to females, suggest that changes are not simply a function of natural selection for different phenotypic optima, or reduced phenotypic variance, across environments. The large body and head size of *G. galloti* males is thought to reflect male – male competition (Molina-Borja et al. 1997, Herrel et al. 1999, Huyghe et al. 2005, Lopez-Darias et al. 2014), while female head size across *Gallotia* varies with prey size and hardness (Lopez-Darias et al. 2014). Based on a link between head size, bite force and diet in females, but a decoupling of bite force and diet in males, Lopez-Darias et al. (2014) concluded that male *Gallotia* morphology is driven by sexual selection and female morphology by natural selection. If differences in the direction of natural selection were solely responsible for shifts in morphospace among populations, then females should have responded at least as strongly, if not more so, than males. Instead, the stronger response of males suggests a possible gradient in the strength of sexual selection across environments. For example, the strength of (or responses to) sexual selection may be stronger in warm, aseasonal environments on Tenerife than in harsh, high elevation locales, where the need to cool and warm

quickly during substantial daily and annual temperature fluxes (Ashton and Feldman 2003, Sears and Angilletta 2004), may be more important. Such a scenario would suggest that, at low elevations, natural and sexual selection act in concert (e.g. Irschick et al. 2008), but may oppose each other at high elevations. Suggestively, relative head size of males tended to increase at high elevations, suggesting that male head size may still be under selection despite smaller body sizes.

The above interpretation relies on trait values reflecting adaptive processes in different environments. However, it is entirely possible that the morphological variation observed here along environmental gradients could be non-adaptive (Angilletta et al. 2004, Sears and Angilletta 2004). Lower resource availability and/or activity time at high elevations could reduce growth rates and body size, especially if juvenile mortality is high (Sears and Angilletta 2004). Evidence in *Anolis* lizards suggests that male growth can be affected by resource constraints more than females, reducing sexual size dimorphism in resource-limited environments (Cox and Calsbeek 2010). Thus, the environmentally structured morphological variation in male *G. galloti* lizards may reflect plastic responses that prevent males from reaching large body sizes, rather than variation in the strength of selection (natural or sexual) through environmental and geographic space.

In addition to potential shifts in the trait optimum among environments, we also found evidence that there is stronger environmental filtering, leading to greater trait clustering, at the highest elevations. Strong filtering in this environment is consistent with the hypothesis that harsh environments (such as those at high elevations or latitudes) limit the range of traits or strategies that can occur (Weiher and Keddy 1995, Weiher et al. 1998, Cornwell et al. 2006, Swenson et al. 2012). High elevation environments (e.g. summit scrub) in Tenerife are characterized by cool average temperatures, low productivity and marked temperature variability, with frost and snow common during winter months (Zobel et al. 2011). Recent volcanic activity may also have contributed to environmental harshness and has been hypothesized to reduce lizard body sizes (Muñoz and Hewlett 2011). The environmental filter operating at high elevations seems to especially exclude large males (Figs. 3 & 5). Such an asymmetric environmental filter could also contribute to a shift in a population's centroid, even if the

actual trait optimum does not shift. Under this scenario, we would expect the distribution of male body sizes at high elevations to appear truncated, or strongly left-skewed, because of the absence of large males. However, we see no obvious skew in the male body size distributions at high elevations (Figure A4), suggesting that the observed centroid shift is not solely a function of asymmetric filtering, and that both shifts and filtering are operating at higher elevations. Variation in filtering likely arises from the same processes hypothesized above: selection against large males and/or plastic responses due to restricted activity times, lower temperatures, and lower resource availability.

Intraspecific morphological diversification in response to spatially varying environmental pressures, i.e. ecological diversification, may presage genetic isolation and speciation (Thorpe et al. 2010, Muñoz et al. 2013). *G. galloti* on the main island of Tenerife, i.e. excluding islets, has traditionally been divided into two subspecies, *G. g. galloti* and *G. g. eisentrauti*. Roughly speaking, the former inhabits southern environments on Tenerife, while the latter inhabits the north, including our Environment C (Thorpe and Baez 1987). However, our results suggest that lizards from Environment C were not morphologically exceptional, thus morphological diversification pressures in *G. galloti* have likely not driven sub-species formation, which instead may reflect historical isolation on precursor islands (Thorpe et al. 1996) or differentiation of other traits not measured here, such as colouration (Molina-Borja et al. 1997, 2006). Lizards from Environment C, especially males, did tend to be large (Fig. 3, also see Molina-Borja et al. 1997), but so did individuals of *G. g. galloti* in Environment A. Environment C also contributed the most to overall morphological dissimilarity, probably because it had the most variable body sizes (Fig. 3), but did not display significant clustering or centroid displacement. Instead, the primary axis of morphological differentiation of *G. galloti* on Tenerife was between the sexes, and secondarily along the island's elevation gradient. Sexual dimorphism can inhibit lineage diversification because dimorphic males and females may use a wider range of ecological resources (Bolnick and Doebeli 2003). Thus the substantial sexual dimorphism of *G. galloti* could have inhibited speciation within Tenerife, though a small island size (Losos and Schluter 2000) and short time for speciation have also likely played a role.

Identifying how environmental variation generates morphological diversity and differentiation among populations can provide a window into the embryonic stages of ecological diversification and, possibly, ecological speciation (Thorpe et al. 2010, Muñoz et al. 2013). We found that environmental variation induces shifts in the position of populations in morphospace and in the volume of morphospace occupied. However, natural selection does not act alone in generating intraspecific morphological diversity across environments; sexual selection may play a role, alongside non-adaptive responses that primarily affect sexually selected traits. Nonetheless, without direct measures of sexual selection in the field, these remain untested hypotheses. Our results also demonstrate that the strength of trait clustering, along with spatial trait-environment relationships, can differ between sexes. Moving forward, explicitly considering sex differences in such analyses will provide new insights into the processes influencing ecological radiation (Butler et al. 2007, Pincheira-Donoso et al. 2009). Lastly, studies that have evaluated trait clustering or evenness to infer assembly processes using just a single sex may have missed key aspects of the structure of trait variation and the processes driving it.

ACKNOWLEDGEMENTS

Thanks to Jorge Lobo for sharing the Tenerife climate and elevation data. Leslie Bode provided assistance in the field and Yoel Stuart provided useful advice. James Hicks and the rest of the University of Nottingham's BEER (biogeography, ecology and evolution research) group provided valuable feedback on earlier drafts. MLD was supported by the EU Seventh Framework Programme (FP7/2007-2013) in the form of a Marie Curie International Outgoing Fellowship.

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Table 1. Eigenvectors for the first three principal components from a principal components analysis on lizard morphology after varimax rotation. Right legs were measured and toe measurements were taken on the fourth toe on the right side. Head traits are shown in Fig. A3.

Variable (residuals)	PC1	PC2	PC3
femur	-0.043	-0.079	0.428
tibia	-0.099	-0.312	0.263
hindtoe	-0.028	-0.567	0.070
humerus	0.071	0.051	0.618
ulna	-0.020	-0.085	0.488
foretoe	-0.053	-0.552	-0.036
head length	-0.401	-0.074	-0.061
pileus width	-0.349	0.304	0.131
head height	-0.362	0.322	0.114
head width	-0.294	0.124	0.195
snout length	-0.410	-0.127	-0.200
lower jaw I	-0.401	-0.139	-0.088
lower jaw II	-0.387	-0.094	-0.033

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Table 2. Wald F -test results for terms in linear mixed effects models evaluating morphological differences between *Gallotia galloti* in different environments and between sexes on Tenerife. When the ENV×SEX interaction was not significant ($\alpha = 0.05$), a reduced model was fitted. All tests are based on marginal sums of squares. The models for head size incorporated unequal variances among environment because AIC_c indicated this provided better fit than assuming equal variances (this was not the case for the other traits).

Trait	ENV			SEX			ENV×SEX		
	F	df	P	F	df	P	F	df	P
Full Model									
log(SVL)	0.86	3,16	0.48	1837.75	1,328	<0.01	7.69	3,328	<0.01
Head Size (PC1)	4.37	3,16	0.020	26.81	1,328	<0.01	1.21	3,328	0.31
Toe Length (PC2)	1.32	3,16	0.30	1.83	1,328	0.18	0.43	3,328	0.73
Leg Length (PC3)	4.78	3,16	0.015	14.23	1,328	<0.01	0.13	3,328	0.94
Reduced Model									
log(SVL)	-	-	-	-	-	-	-	-	-
Head Size (PC1)	4.33	3,16	0.021	26.78	3,331	<0.01	-	-	-
Toe Length (PC2)	1.34	3,16	0.29	1.84	1,331	0.18	-	-	-
Leg Length (PC3)	4.74	3,16	0.015	14.35	1,331	<0.01	-	-	-

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FIGURE LEGENDS

Figure 1. Male (upper) and female (lower) *Gallotia galloti* on Tenerife. Images are scaled so that head length approximately matches the mean difference among males and females.

Figure 2. Four environmental zones on Tenerife generated using *k*-means clustering on climate, elevation and aspect at 500m resolution, accounting for 70% of the environmental variation on the island. Blue diamonds indicate sampling localities.

Figure 3. Male and female traits in four different environments on Tenerife. Head size, toe length and leg length are all corrected for body size (SVL). Environment letters correspond to the map in Figure 2. Principal component loadings are given in Table 2.

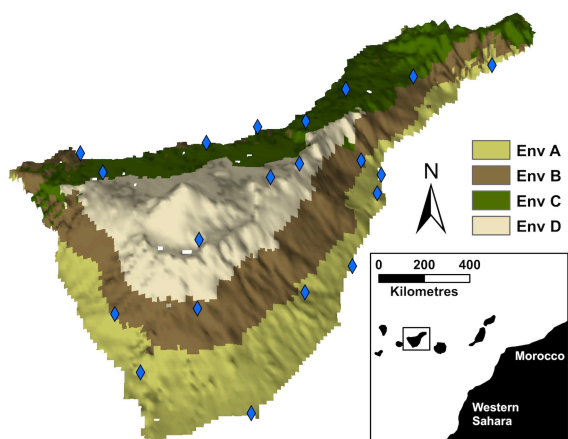
Figure 4. Morphospace occupied by male and female *Gallotia galloti* on Tenerife. Convex hulls were drawn using twenty randomly chosen males and twenty randomly chosen females. SVL is log snout-vent length, -HS is head size (negatively scaled so that small values equal small heads), and LL is leg length. All axes were standardized to zero mean and unit variance.

Figure 5. The position and volume of morphospace occupied by populations of *Gallotia galloti* in different environments on Tenerife. Column one shows the convex hulls of populations from the four environments (A – D in Figure 3), column two shows the convex hull volume for lizards from each environment, and column three depicts the distance of the population's morphospace centroid from the centroid when all populations were pooled. Rows show results for both sexes pooled, and males and females only. Values are based on 20 randomly chosen males and females from each environment. ** indicates a P-value less than 0.05 based on our null model. * indicates a P-value with a 95% confidence interval that spans 0.05. SVL is log snout-vent length, -HS is head size (negatively scaled so that small values equal small heads), and LL is leg length. All axes were standardized to zero mean and unit variance.

Figure 1

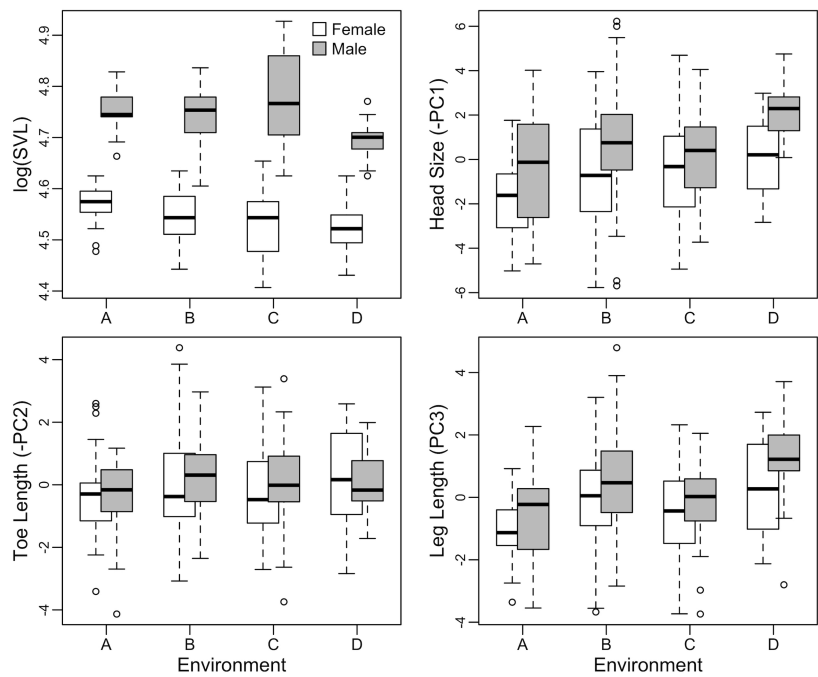


Figure 2



673 Figure 3

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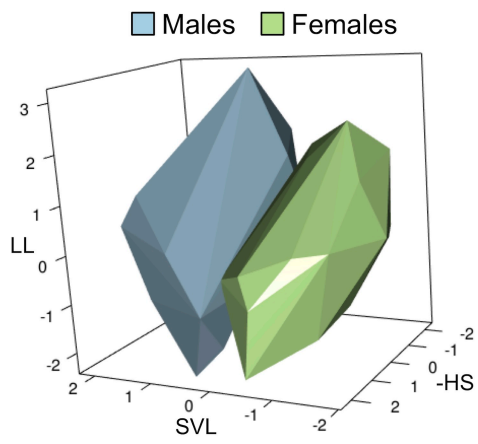
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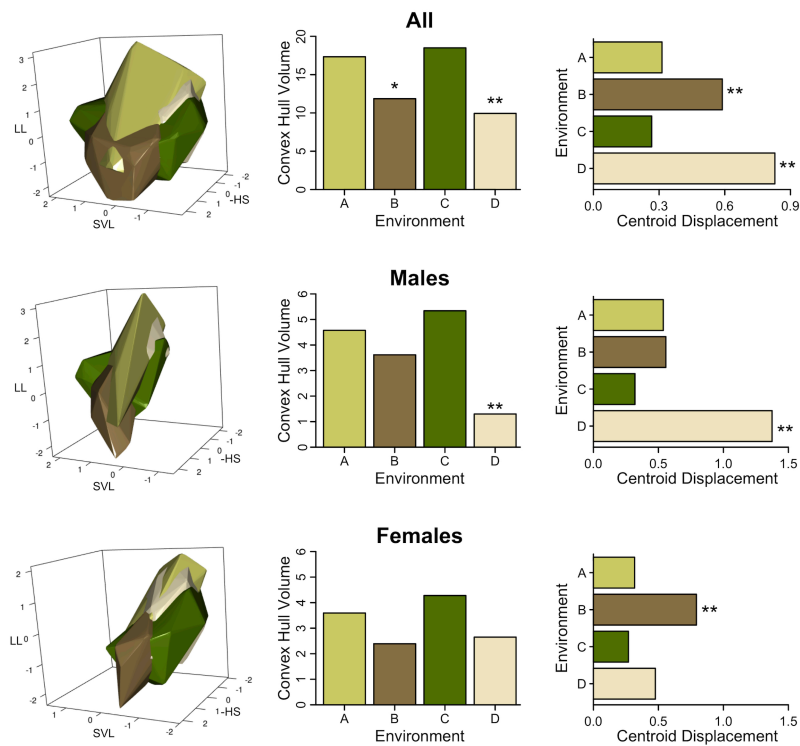
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Figure 4



685 Figure 5

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