1 **TITLE**
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3 **Sex-specific responses of phenotypic diversity to environmental variation**
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23 **ABSTRACT**

24 Identifying the factors generating ecomorphological diversity within species can provide a window

25 into the nascent stages of ecological radiation. Sexual dimorphism is an obvious axis of intraspecific

26 morphological diversity that could affect how environmental variation leads to ecological divergence

27 among populations. In this paper we test for sex-specific responses in how environmental variation

28 generates phenotypic diversity within species, using the generalist lizard *Gallotia galloti* on Tenerife

29 (Canary Islands). We evaluate two hypotheses: the first proposes that different environments have

30 different phenotypic optima, leading to shifts in the positions of populations in morphospace between

31 environments; the second predicts that the strength of trait-filtering differs between environments,

32 predicting changes in the volume of morphospace occupied by populations in different environments.

33 We found that intraspecific morphological diversity, provided it is adaptive, arises from both shifts in

34 populations' position in morphospace and differences in the strength of environmental filtering among

35 environments, especially at high elevations. However, effects were found only in males;

36 morphological diversity of females responded little to environmental variation. These results within

37 *G. galloti* suggest natural selection is not the sole source of phenotypic diversity across environments,

38 but rather that variation in the strength of, or response to, sexual selection may play an important role

39 in generating morphological diversity in environmentally diverse settings. More generally, disparities

40 in trait-environment relationships among males and females also suggest that ignoring sex differences

41 in studies of trait dispersion and clustering may produce misleading inferences.

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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

71   insight into the factors driving ecological function and dynamics within communities (Bolnick et al.

72   2011, Violle et al. 2012).

73

74   As populations diversify, they can fill ecological space in new ways. Specifically, environments may

75   differ in their ecological optima, leading to directional selection and shifts in a population's position

76   within ecological space. For example, Caribbean *Anolis* lizards have repeatedly evolved toward

77   different phenotypic optima depending on their microhabitat use (Mahler et al. 2013). Environments

78   may also differ in the range of ecological variation they can support, i.e. in the strength of the

79   environmental filter they impose (Weiher et al. 1998, Cornwell et al. 2006, Violle et al. 2012),

80   constraining the volume of ecological space occupied by a species, or population (Weiher et al. 1998,

81   Cornwell et al. 2006, Algar et al. 2011, Violle et al. 2012). These two options are not mutually

82   exclusive and could act in concert or opposition to influence how populations fill ecological space

83   across heterogeneous environments.

84

85   Sexual dimorphism is a fundamental axis of morphological variation in animals (e.g. Fairbairn et al.

86   2007) and may contribute substantially to ecological and lineage diversification in a number of ways.

87   Sexual selection, which can produce sexual size dimorphism via male-male competition or fecundity

88   selection in females (Cox et al. 2003), has been identified as a driver of speciation (Panhuis et al.

89   2001, Hudson and Price 2014). However, sexual dimorphism may also inhibit diversification if males

90   and females of dimorphic species use a wide range of resources (Bolnick and Doebeli 2003, Ritchie

91   2007). Sexual dimorphism may also reflect both natural and sexual selection: Lopez-Darias et al.

92   (2014) showed, in *Gallotia* lizards in the Canary Islands, that the same traits (head size and bite force)

93   may be under sexual selection for one sex (males) and natural selection for the other (females).

94   Regardless of whether dimorphism arose from sexual or natural selection, morphological differences

95   between males and females can translate into ecological differences (Schoener 1967, Shine 1989,

96   Butler et al. 2000, Butler and Losos 2002, Bolnick et al. 2011), raising the possibility that males and

97   females may respond differentially to environmental variation. For example, Butler & Losos (2002)

98   found that *Anolis* ecomorphs in different microhabitats also varied in their degree of sexual

dimorphism. Similarly, habitat × 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 km^2 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

127   part from the influence of elevation and orientation with respect to the humid northeast trade winds

128   (Fernández-Palacios and Nicolás 1995, Fernández-Palacios and Whittaker 2008). Although human

129   habitat modification, primarily through agriculture and tourism-related development, has greatly

130   reduced the extent of most natural habitats, it has also generated agricultural and urban habitats at the

131   regional scale (Fernández-Palacios and Whittaker 2008).

132

133   Although Tenerife (and the Canaries more generally) harbours several stunning evolutionary

134   radiations, especially of plants and arthropods (e.g. Arnedo et al. 2001, Arechavaleta et al. 2009,

135   Vitales et al. 2014), the lizard fauna has not radiated extensively within islands (Cox et al. 2010). Just

136   four native lizard species inhabit Tenerife: one endemic gecko, one endemic skink, and two extant

137   lacertid species of the endemic Canarian genus, *Gallotia*. Of these, *G. galloti* is by far the most

138   widespread and abundant. Its only extant putative lizard competitor, *G. intermedia*, is extremely

139   geographically restricted, limited to a small area of cliff habitat. Thus, despite Tenerife's substantial

140   environmental diversity, its herpetofauna is dominated by a single, widespread species.

141

142   *G. galloti* is a medium sized, omnivorous lizard (Fig. 1), restricted to Tenerife and La Palma and is

143   one of the dominant and most conspicuous native vertebrates on both islands. *G. galloti*'s ancestor

144   likely colonized Tenerife's proto-islands 9-10 mya (Cox et al. 2010) and it currently occupies every

145   major habitat and geographical region in Tenerife, though its abundance in the northern tip of the

146   island, Anaga, seems to be markedly lower than elsewhere (Thorpe and Baez 1987). It and its

147   congeners are sexually dimorphic, especially in body size (males are larger), but also, for most

148   species, in body shape, limb length and head size (Thorpe and Baez 1987, Molina-Borja et al. 1997,

149   2010, Herrel et al. 1999, Molina-Borja 2003, Lopez-Darias et al. 2014).

150

151   In addition to substantial sexual dimorphism, *G. galloti* also exhibits extensive morphological

152   variation through space. Thorpe and Baez (1987) surveyed 18 populations of *G. galloti* across

153   Tenerife and identified considerable geographical variation in body and head size, scalation and

154   colour. However, geographical concordance across sexes and traits varied considerably. For example,

155   body size showed very different patterns in males and females, while head size varied similarly

156   between sexes (though males had larger heads). Traditionally, phenotypic differences have led to the

157   delineation of two subspecies (or races) on the island (*G. galloti galloti* and *G. galloti eisentrauti*) that

158   differ in colouration (Thorpe and Baez 1987, Molina-Borja et al. 1997). *Gallotia g. eisentrauti* also

159   tends to be larger (Molina-Borja et al. 1997), though this difference is less clear when variation in *G.*

160   *g. gallotia* due to contact zones and elevation is incorporated in the comparison (Thorpe and Baez

161   1987).

162

Quantifying environmental variation

164   We identified areas of similar environmental conditions on Tenerife, following the approach used by

165   Hortal and Lobo (2005) and Hortal et al. (2007). Firstly, because climatic variables tend to be

166   correlated through space, we performed a principal component analysis on climate and topographic

167   variables sampled at a 500m resolution across. We included the following variables: elevation, aspect,

168   and mean annual, maximum and minimum temperature and annual, monthly minimum and maximum

169   precipitation (Fig. A1; raw data from Hortal et al. (2006), shared by J.M. Lobo). For aspect, we

170   computed 'northness' [northness = cosine(aspect)] and 'eastness' [eastness = sine(aspect)], where

171   aspect is measured in radians. We extracted the first three principal components for the subsequent

172   clustering analysis. Environmental PCs 1-3 accounted for 88% of the total variance (Table A1) and

173   co-varied with temperature and elevation (envPC1), aridity and northness (envPC2) and eastness

174   (envPC3), respectively. These captured the three major axes of environmental and ecosystem

175   variation on Tenerife (Fig. A2).

176

177   We used k-means clustering of environmental PCs 1-3 to delineate environmental zones on Tenerife.

178   We used k = 4 as this captured 70% of the environmental variation on Tenerife with a tractable

179   number of environmental zones to encompass variation in our model organism (Fig. 2). Environment

180   A is found at low southern elevations characterized by high temperatures and low rainfall.

181   Environment B is found at mid elevations, with southern exposure, cooler temperatures and more

182   rainfall than Environment A. Environment C represents the north of the island at low to mid

183   elevations, and has northerly slopes with much higher rainfall and humidity due to the influence of the

184   trade-winds. Environment D is found at the highest elevations on the Teide volcano, and is

185   characterized by extreme temperatures, especially cold, and widely seasonal precipitation patterns

186   (including snow).

187

188   Lizard sampling

189   We sampled lizards in August 2011 at 20 sites across Tenerife. Sites were representative of the major

190   environmental zones (Fig. 2). At each location, we trapped lizards for one to four consecutive days

191   using pitfall traps baited with tomato or banana. After we measured them, lizards were released

192   precisely where they were caught. Captured lizards were temporarily marked with a marker pen on

193   the abdomen to avoid re-measuring the same individual. At each site, we aimed to trap 10-12 lizards

194   of each sex (identified by appearance and/or everting hemipenes or checking the abdomen for eggs).

195   Individuals that could not be reliably sexed (e.g. females versus juvenile males) were excluded. At

196   some sites, the target sample size could not be obtained, while at others, high abundance meant more

197   lizards could be measured (Table A2).

198

199   Quantifying morphological variation

200   We measured 14 traits relating to body size (snout-vent length; SVL), leg and toe length, and head

201   length, height and width (Table 1; Fig. A3). MLD performed all measurements to eliminate measurer

202   effects. To account for the effect of body size, we regressed the logarithm of each trait on log SVL

203   and used the residuals in subsequent analyses (e.g. Pinto et al. 2008). Next, we identified key axes of

204   morphological variation using a principal component analysis on these residuals (Table A3). We

205   retained the first three principal components, which accounted for 73% of the total variance (Table

206   A3; PC1 = 54.3%, PC2= 11.4%, PC3=7.2%). We used a varimax rotation to clarify the loading

207   structure and increase interpretability. After rotation, PCs 1-3 loaded heavily on head size, toe length,

208   and leg length, respectively (Table 1).

209

210   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

239   compute convex hulls for each environment and their unions. We repeated this analysis for each trait

240   individually, using trait ranges instead of convex hulls. All analyses were carried out with both sexes

241   pooled and for males and females separately.

242

243   To test the environmental filter-strength hypotheses, we compared the convex hull volume for lizards

244   from each environment to the volume expected from a null model. For the optimum-shift hypothesis,

245   we calculated the distance from each population's morphospace centroid to the centroid of all

246   populations pooled and compared this to a null expectation. The null expectation was created for each

247   environment by randomly selecting 40 individuals (20 males and 20 females) without replacement

248   from the entire pool of individuals. We repeated this 1000 times to compute P-values and their 95%

249   confidence intervals following Ruxton and Neuhäuser (2013), with the observed value included in

250   both the numerator and denominator of P-value calculations. All tests were two-tailed.

251

252   **RESULTS**

253   **Testing for trait and sexual dimorphism variation across environments**

254   We found considerable sexual size dimorphism in *Gallotia galloti*, with males achieving much greater

255   SVL than females (Figs. 3 and 4). However, we also found a significant interaction between sex and

256   environment in our linear mixed effects model (Table 2; $F_{3,328} = 7.69$, $P < 0.001$) indicating that the

257   degree of sexual size dimorphism varied among environments. No other traits showed a significant

258   sex × environment interaction (Table 2). Models assuming equal variances among environments had

259   lower AIC_c values than models that allowed variances to vary for all traits except head size (PC1

260      $\Delta AIC_c = 5.6$). Thus for this trait, we present results from models allowing unequal variances among

261   environments. Results were nearly identical (and there were no changes in significance) regardless of

262   which models were used.

263

264   Once the sex × environment interaction was removed, we found significant sexual dimorphism in

265   head size (PC1) and leg length (PC3), but not toe length (PC2; Table 2). Males tended to have larger

266   heads and longer legs, relative to body size, than females. Head size (PC1) and leg length (PC3) also

267   varied across environments, independently of sex, (P =< 0.02 for both; Table 2). The trend was for

268   greater relative male head size and longer relative leg lengths at high elevations (Environment D; Fig.

269   3).

270

271   **Environmental variation and morphological dissimilarity**

272   Morphological dissimilarity, i.e. the percentage of morphospace uniquely occupied by lizards from a

273   single environment, was 36% (Fig. 5), but this was not significant based on our null model ($P = 0.15$,

274   $CI_{95} = 0.13–0.18$). Individual contributions of environments to this value ranged from 3% to 17%

275   (Table A4), but only Environment C's unique volume differed significantly from the null expectation,

276   though the 95% confidence interval still overlapped 0.05 ($P = 0.041$, $CI_{95} = 0.029–0.053$). Pairwise

277   dissimilarity (i.e. morphological turnover) among environments ranged from 51% – 74%, but only

278   comparisons involving the high elevation Environment D were significant (Table A5).

279

280   Partitioning the data by sex revealed different patterns among males and females. Males underwent

281   more morphological turnover between environments than females (61% versus 42%). Moreover, for

282   males, this morphological turnover was significant ($P = 0.023$, $CI_{95} = 0.014–0.032$) while for females

283   it was not ($P = 0.43$, $CI_{95} = 0.39–0.45$). However, uniquely occupied volumes were not significant for

284   any environment for either males or females, though P-values were low for Environment C (Table

285   A4), suggesting no single environment drives morphological dissimilarity. Pairwise morphological

286   dissimilarity for males was higher than for females. For the former, all environments differed

287   significantly from Environment D, while for females only Environments B (mid elevation) and D

288   (high elevation) differed significantly (Table A5).

289

290   **Individual trait dissimilarity among environments**

291   When sexes were pooled, individual trait dissimilarity was 20% for body size (log SVL), 14% for

292   head size (PC1) and 11% for leg length (PC3), though only body size dissimilarity was significant (P

293   $= 0.004$, $CI_{95} = 0.000088–0.0008$). Males and females both showed greater dissimilarity for body size

11

294   than other traits, with males having greater dissimilarity than females for all traits. However, only

295   male body size dissimilarity was significant (Table A6; $P = 0.002$, $CI_{95} = 0.001–0.0048$).

296

297   With sexes pooled, the only significant pairwise comparisons were for body size turnover between

298   environments B versus D, C versus D, and B versus C (Table A7). However, for males, several

299   significant pairwise differences were found for both body size (Table A7; B versus D, and C versus

300   D) and head size (Table 6; Environment D differed from all others). For females, body size turnover

301   was not significant and only a single comparison was significant for leg length (Table A7;

302   Environment B versus D).

303

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

305   When both sexes were considered together, populations at mid and high elevations (Environments B

306   and D in Fig. 2) occupied less morphospace than lower elevation environments (Fig. 5). This

307   clustering was strongest and significant at the highest elevations (Environment D; $P = 0.011$, $CI_{95} =$

308     $0.0045–0.017$), but weak at mid elevations (Environment B; Fig. 5; $P = 0.058$, $CI_{95} = 0.043–0.072$)..

309   Neither the low elevation northern or southern environments (Environments A and C) displayed

310   significant clustering ($P > 0.75$ for both). Males occupied significantly less morphospace, i.e. were

311   more clustered, at high elevations (Environment D) than expected due to chance (Fig. 5; $P = 0.033$,

312     $CI_{95} = 0.022–0.044$), but were not clustered in any other environment ($P > 0.30$ in all cases). Although

313   patterns of females appeared qualitatively similar to those of males, they exhibited less variation and

314   displayed no significant clustering in any environment (Fig. 5; $P > 0.12$ in all environments).

315

316   Pooling both sexes, the mid and high elevation environments (B and D, respectively) showed greater

317   centroid displacement than the two low elevation environments. Of the former set, Environment D

318   was more severely displaced (Fig 5; $P = 0.001$, $CI_{95} = 0.001–0.0029$) relative to the null expectation

319   than the lower elevation Environment B (Fig. 5; $P = 0.006$, $CI_{95} = 0.0012–0.011$). Once again, the

320   strong departure of the high elevation Environment D was driven by male variation (Fig. 5). Males

321   from Environment D were much further from the pooled morphospace centroid than expected from

322   our null model (P = 0.002, CI$_{95}$ = 0.001–0.0048). Females show no such displacement at the highest

323   elevations, but did for the mid-elevation Environment B (Fig. 5; P = 0.002, CI$_{95}$ = 0.001–0.0048)

324

325

DISCUSSION

326

327   Identifying how environmental factors generate ecomorphological variation within species provides a

328   window into the nascent stages of ecological radiation. On Tenerife, just over one third of the

329   morphospace occupied by the lizard *Gallotia galloti* (Lacertidae) was uniquely occupied by lizards

330   from a single environment, indicating that environmental differences are accompanied by

331   morphological turnover (*sensu* Villéger et al. 2011) among populations. We tested two pathways by

332   which environmental variation may have generated these differences between populations within a

333   species, and thus enhance morphological diversity. The optimum-shift hypothesis proposes that the

334   phenotypic optimum differs between environments, leading to divergence in ecomorphological traits

335   between populations in different environments (Mahler et al. 2013). The environmental filter-strength

336   hypothesis suggests that the strength of environmental filtering varies across environments, leading to

337   differential trait-clustering (Weiher et al. 1998, Algar et al. 2011, Swenson et al. 2012). Thus, under

338   an optimum-shift model, environment-specific selection pressures act primarily on phenotypic

339   position in morphospace, while under an environmental filter-strength model, they act primarily on

340   phenotypic variance.

341

342   We found that populations' morphospace volumes and centroid displacements (the distance of a

343   population's centroid in morphospace from the overall centroid) varied among environments, and that

344   this variation was elevationally structured. At low elevations (Environments A and C in Figure 3),

345   neither morphospace volume nor centroid displacement differed from that expected based on random

346   sampling from the total population. However, at mid to high elevations (Environments B and D),

347   populations' morphospace volumes were less and centroid displacements were greater than the null

348   expectation, suggesting an increase in trait clustering at high elevations and a shift in trait optimums.

349

13

350 However, the intraspecific morphological diversity observed in *G. galloti* across environments arose

351 from environmentally structured morphological variation in males, but not in females. Variation in

352 male lizards across environments primarily occurred along the body size axis, with weak variation in

353 leg length and head size. Males tended to be smaller at high elevation, a common, but not ubiquitous,

354 pattern within lizards (Ashton and Feldman 2003, Pincheira-Donoso and Meiri 2013, Muñoz et al.

355 2014a). In contrast, we found that female patterns of morphospace occupation did not differ from

356 random expectations, with the single exception of centroid displacement in Environment B. Thorpe

357 and Baez (1987) suggested that geographical patterns of male and female body size on Tenerife were

358 incongruent. Our findings suggest that these differences—and concomitant changes in sexual

359 dimorphism—arise, at least in part, from reduced morphological differentiation of females among

360 environments, compared to males. This pattern is consistent with the phenomenological Rensch's

361 rule, which suggests greater size variation among males than females (Blanckenhorn et al. 2006).

362

363 Although our results are consistent with both the optimum-shift and environmental-filter strength

364 hypotheses, the discrepancy between male and female variation reveals a more complex story. The

365 larger shifts in morphospace position of *G. galloti* males, relative to females, suggest that changes are

366 not simply a function of natural selection for different phenotypic optima, or reduced phenotypic

367 variance, across environments. The large body and head size of *G. galloti* males is thought to reflect

368 male – male competition (Molina-Borja et al. 1997, Herrel et al. 1999, Huyghe et al. 2005, Lopez-

369 Darias et al. 2014), while female head size across *Gallotia* varies with prey size and hardness (Lopez-

370 Darias et al. 2014). Based on a link between head size, bite force and diet in females, but a decoupling

371 of bite force and diet in males, Lopez-Darias et al. (2014) concluded that male *Gallotia* morphology is

372 driven by sexual selection and female morphology by natural selection. If differences in the direction

373 of natural selection were solely responsible for shifts in morphospace among populations, then

374 females should have responded at least as strongly, if not more so, than males. Instead, the stronger

375 response of males suggests a possible gradient in the strength of sexual selection across environments.

376 For example, the strength of (or responses to) sexual selection may be stronger in warm, aseasonal

377 environments on Tenerife than in harsh, high elevation locales, where the need to cool and warm

378   quickly during substantial daily and annual temperature fluxes (Ashton and Feldman 2003, Sears and

379   Angilletta 2004), may be more important. Such a scenario would suggest that, at low elevations,

380   natural and sexual selection act in concert (e.g. Irschick et al. 2008), but may oppose each other at

381   high elevations. Suggestively, relative head size of males tended to increase at high elevations,

382   suggesting that male head size may still be under selection despite smaller body sizes.

383

384   The above interpretation relies on trait values reflecting adaptive processes in different environments.

385   However, it is entirely possible that the morphological variation observed here along environmental

386   gradients could be non-adaptive (Angilletta et al. 2004, Sears and Angilletta 2004). Lower resource

387   availability and/or activity time at high elevations could reduce growth rates and body size, especially

388   if juvenile mortality is high (Sears and Angilletta 2004). Evidence in *Anolis* lizards suggests that male

389   growth can be affected by resource constraints more than females, reducing sexual size dimorphism in

390   resource-limited environments (Cox and Calsbeek 2010). Thus, the environmentally structured

391   morphological variation in male *G. galloti* lizards may reflect plastic responses that prevent males

392   from reaching large body sizes, rather than variation in the strength of selection (natural or sexual)

393   through environmental and geographic space.

394

395   In addition to potential shifts in the trait optimum among environments, we also found evidence that

396   there is stronger environmental filtering, leading to greater trait clustering, at the highest elevations.

397   Strong filtering in this environment is consistent with the hypothesis that harsh environments (such as

398   those at high elevations or latitudes) limit the range of traits or strategies that can occur (Weiher and

399   Keddy 1995, Weiher et al. 1998, Cornwell et al. 2006, Swenson et al. 2012). High elevation

400   environments (e.g. summit scrub) in Tenerife are characterized by cool average temperatures, low

401   productivity and marked temperature variability, with frost and snow common during winter months

402   (Zobel et al. 2011). Recent volcanic activity may also have contributed to environmental harshness

403   and has been hypothesized to reduce lizard body sizes (Muñoz and Hewlett 2011). The environmental

404   filter operating at high elevations seems to especially exclude large males (Figs. 3 & 5). Such an

405   asymmetric environmental filter could also contribute to a shift in a population's centroid, even if the

406   actual trait optimum does not shift. Under this scenario, we would expect the distribution of male

407   body sizes at high elevations to appear truncated, or strongly left-skewed, because of the absence of

408   large males. However, we see no obvious skew in the male body size distributions at high elevations

409   (Figure A4), suggesting that the observed centroid shift is not solely a function of asymmetric

410   filtering, and that both shifts and filtering are operating at higher elevations. Variation in filtering

411   likely arises from the same processes hypothesized above: selection against large males and/or plastic

412   responses due to restricted activity times, lower temperatures, and lower resource availability.

413

414   Intraspecific morphological diversification in response to spatially varying environmental pressures,

415   i.e. ecological diversification, may presage genetic isolation and speciation (Thorpe et al. 2010,

416   Muñoz et al. 2013). *G. galloti* on the main island of Tenerife, i.e. excluding islets, has traditionally

417   been divided into two subspecies, *G. g. galloti* and *G. g. eisentrauti*. Roughly speaking, the former

418   inhabits southern environments on Tenerife, while the latter inhabits the north, including our

419   Environment C (Thorpe and Baez 1987). However, our results suggest that lizards from Environment

420   C were not morphologically exceptional, thus morphological diversification pressures in *G. galloti*

421   have likely not driven sub-species formation, which instead may reflect historical isolation on

422   precursor islands (Thorpe et al. 1996) or differentiation of other traits not measured here, such as

423   colouration (Molina-Borja et al. 1997, 2006). Lizards from Environment C, especially males, did tend

424   to be large (Fig. 3, also see Molina-Borja et al. 1997), but so did individuals of *G. g. galloti* in

425   Environment A. Environment C also contributed the most to overall morphological dissimilarity,

426   probably because it had the most variable body sizes (Fig. 3), but did not display significant clustering

427   or centroid displacement. Instead, the primary axis of morphological differentiation of *G. galloti* on

428   Tenerife was between the sexes, and secondarily along the island's elevation gradient. Sexual

429   dimorphism can inhibit lineage diversification because dimorphic males and females may use a wider

430   range of ecological resources (Bolnick and Doebeli 2003). Thus the substantial sexual dimorphism of

431   *G. galloti* could have inhibited speciation within Tenerife, though a small island size (Losos and

432   Schluter 2000) and short time for speciation have also likely played a role.

433

434 Identifying how environmental variation generates morphological diversity and differentiation among

435 populations can provide a window into the embryonic stages of ecological diversification and,

436 possibly, ecological speciation (Thorpe et al. 2010, Muñoz et al. 2013). We found that environmental

437 variation induces shifts in the position of populations in morphospace and in the volume of

438 morphospace occupied. However, natural selection does not act alone in generating intraspecific

439 morphological diversity across environments; sexual selection may play a role, alongside non-

440 adaptive responses that primarily affect sexually selected traits. Nonetheless, without direct measures

441 of sexual selection in the field, these remain untested hypotheses. Our results also demonstrate that

442 the strength of trait clustering, along with spatial trait-environment relationships, can differ between

443 sexes. Moving forward, explicitly considering sex differences in such analyses will provide new

444 insights into the processes influencing ecological radiation (Butler et al. 2007, Pincheira-Donoso et al.

445 2009). Lastly, studies that have evaluated trait clustering or evenness to infer assembly processes

446 using just a single sex may have missed key aspects of the structure of trait variation and the

447 processes driving it.

448

455

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620

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	-	-	-

FIGURE LEGENDS

631

632 Figure 1. Male (upper) and female (lower) *Gallotia galloti* on Tenerife. Images are scaled so that head

633 length approximately matches the mean difference among males and females.

634

635 Figure 2. Four environmental zones on Tenerife generated using *k*-means clustering on climate,

636 elevation and aspect at 500m resolution, accounting for 70% of the environmental variation on the

637 island. Blue diamonds indicate sampling localities.

638

639 Figure 3. Male and female traits in four different environments on Tenerife. Head size, toe length and

640 leg length are all corrected for body size (SVL). Environment letters correspond to the map in Figure

641 2. Principal component loadings are given in Table 2.

642

643 Figure 4. Morphospace occupied by male and female *Gallotia galloti* on Tenerife. Convex hulls were

644 drawn using twenty randomly chosen males and twenty randomly chosen females. SVL is log snout–

645 vent length, -HS is head size (negatively scaled so that small values equal small heads), and LL is leg

646 length. All axes were standardized to zero mean and unit variance.

647

648 Figure 5. The position and volume of morphospace occupied by populations of *Gallotia galloti* in

649 different environments on Tenerife. Column one shows the convex hulls of populations from the four

650 environments (A – D in Figure 3), column two shows the convex hull volume for lizards from each

651 environment, and column three depicts the distance of the population's morphospace centroid from

652 the centroid when all populations were pooled. Rows show results for both sexes pooled, and males

653 and females only. Values are based on 20 randomly chosen males and females from each

654 environment. ** indicates a P-value less than 0.05 based on our null model. * indicates a P-value with

655 a 95% confidence interval that spans 0.05. SVL is log snout-vent length, -HS is head size (negatively

656 scaled so that small values equal small heads), and LL is leg length. All axes were standardized to

657 zero mean and unit variance.

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661   Figure 1

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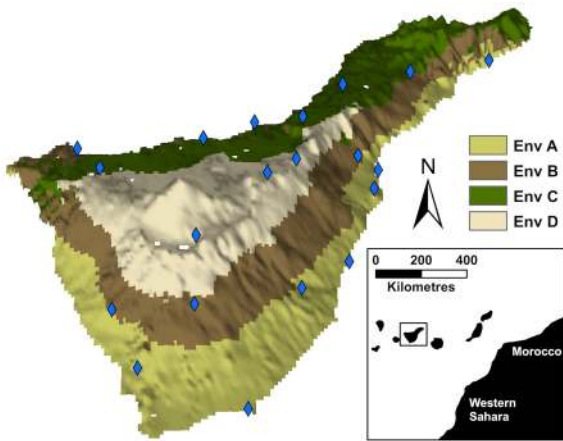663

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667   Figure 2
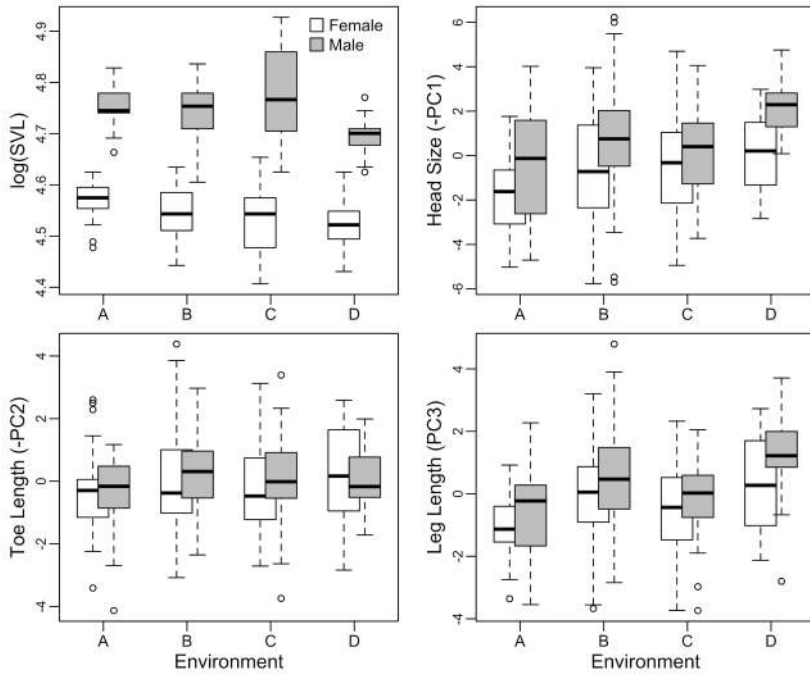
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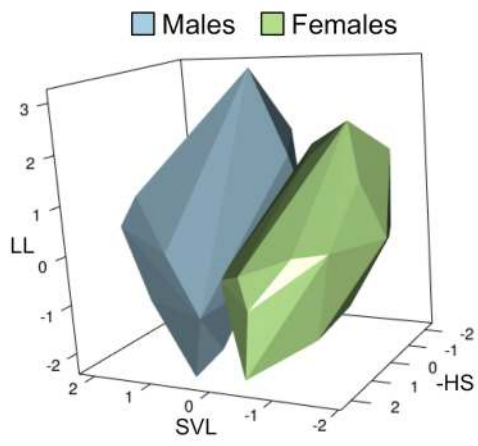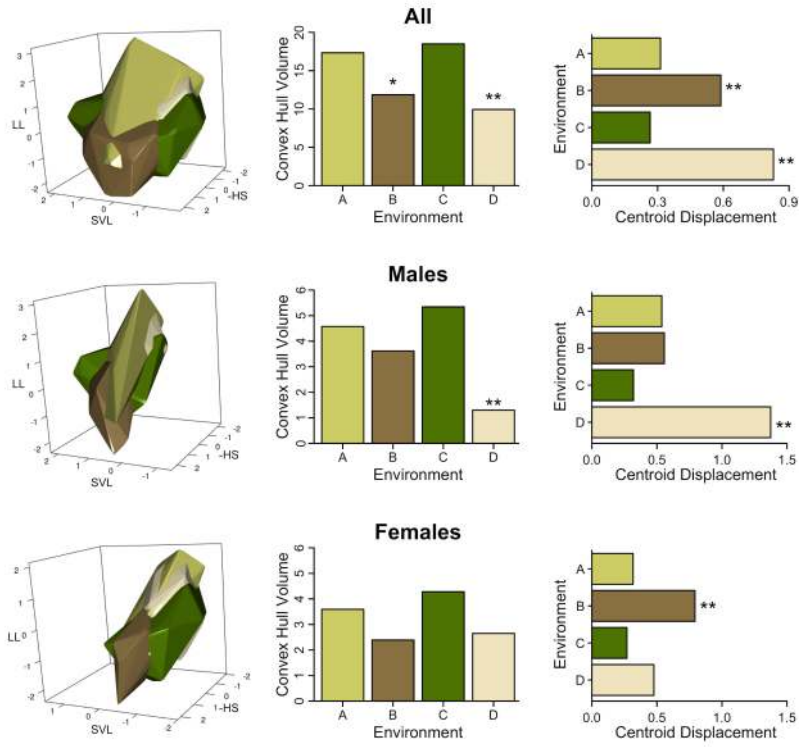672

673   Figure 3

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