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1 **TITLE**

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3 **Sex-specific responses of phenotypic diversity to environmental variation**

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5

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20 **KEYWORDS**

21 Convex hull, ecological radiation, ecomorphology, elevation gradients, environmental filtering,

22 intraspecific variation, lizards, sexual selection, sexual size dimorphism, trait dispersion

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.

42

43

44 **INTRODUCTION**

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

47 Environmental features can both encourage evolutionary radiation, via ecological opportunity
48 (Schluter 2000), or inhibit it, e.g. through insufficient area or heterogeneity (Ricklefs and Lovette
49 1999, Losos and Schluter 2000, Algaer and Mahler 2015). Understanding how, and when,
50 environmental variation influences ecological diversification is thus a key question for evolutionary
51 biologists and ecologists (Blankers et al. 2012, Kaliontzopoulou et al. 2014).

52

53 The relationship between a species' environment and its morphological variability has received
54 substantial attention in a wide variety of lizard groups. For example, limb length is known to be
55 adaptive for improved locomotion on particular substrates, such as narrow versus broad perches
56 (*Anolis*; Losos et al. 2000), open *versus* closed habitats (*Niveoscincus*; Melville and Swain 2000) or
57 terrestrial versus arboreal habitats (chameleons; Bickel and Losos 2002). Other traits, such as head
58 characteristics (Huyghe et al. 2007, Measey et al. 2009) and colour pattern (Forsman and Shine 1995)
59 are also known to differ among environments in lizards. At broader scales, body size shows
60 considerable variability along elevation and latitudinal clines (Ashton and Feldman 2003, Pincheira-
61 Donoso et al. 2008, Muñoz et al. 2014a). Other traits, such as physiological tolerance, visual system,
62 and behavior also vary with environmental conditions in lizards (Leal and Fleishman 2002, Ord et al.
63 2010, Johnson et al. 2010, Muñoz et al. 2014b).

64

65 Studies of morphological variation within clades and communities have traditionally focused on mean
66 differences among species, and thus attempt to reconstruct the drivers of ecological diversification
67 after the fact. An alternative approach is to examine how morphological variation is generated among
68 populations that have not (yet) undergone speciation, providing insight into the nascent stages of
69 ecological diversification and adaptive radiation (Thorpe and Baez 1987, Thorpe et al. 2010). More
70 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

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

108

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

120

121 **METHODS**

122 **Study system**

123 Tenerife, the largest island in the Canary Islands is environmentally very diverse. Covering over
124 2,000 km² and rising to more than 3,700 m above sea level, it hosts a wide range of habitats, including
125 sub-desert coastal scrub, thermophilous, pine and laurel forest, and high elevation scrub/alpine
126 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

163 **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 evert ing 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**

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

219

220 **Testing the optimum-shift and environmental filter-strength hypotheses**

221 We used three morphological axes for the morphospace analysis: SVL (log-transformed), head size
222 (PC1), and leg length (PC3). We omitted toe length (PC2) because we found no differences between
223 environments or sexes in this trait (Table 2). We standardized each trait (logSVL, PC1 and PC3) to
224 have a zero mean and unit variance before computing convex hulls. Estimates of convex hull volume
225 are sensitive to sample size; larger samples are more likely to contain extreme values. To account for
226 unequal sampling across environments, we randomly subsampled 20 males and 20 females from each
227 environment and used these subsets to compute convex hull volumes. We repeated this sub-sampling
228 100 times and used the mean in subsequent analyses.

229

230 We measured the volume of morphospace occupied by lizards from each environment and all
231 environments together using convex hull analysis (Cornwell et al. 2006), where morphospace was
232 defined by three axes: body size, head size and limb length. Our measure of volume is equivalent to
233 the functional richness of a species assemblage (Villéger et al. 2008). Next, we measured the
234 morphological dissimilarity of lizard populations among the four environments, following Villéger et
235 al (2011). The morphological dissimilarity is the percentage of morphospace volume that is occupied
236 uniquely by, in this case, lizards from a single environment. We computed the total morphological
237 dissimilarity among all environments, as well as all six pairwise combinations. We used the
238 '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 \times 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 \times 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

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

326 **DISCUSSION**

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

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

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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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623

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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630 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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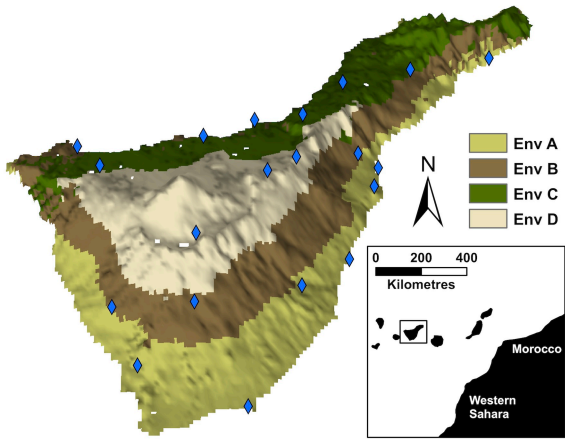
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667 Figure 2

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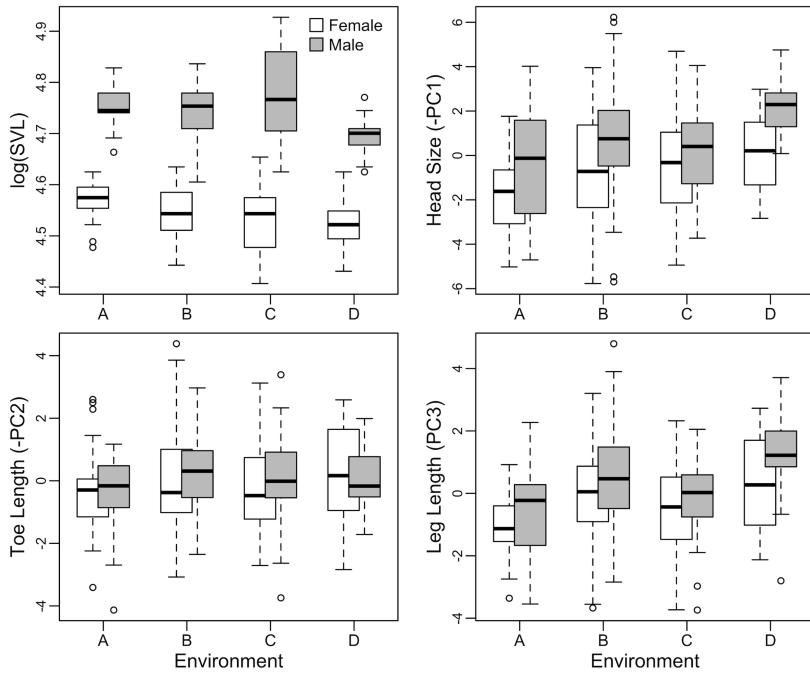
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673 Figure 3

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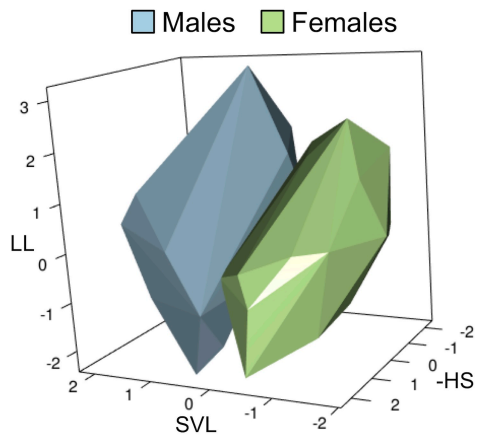
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679 Figure 4

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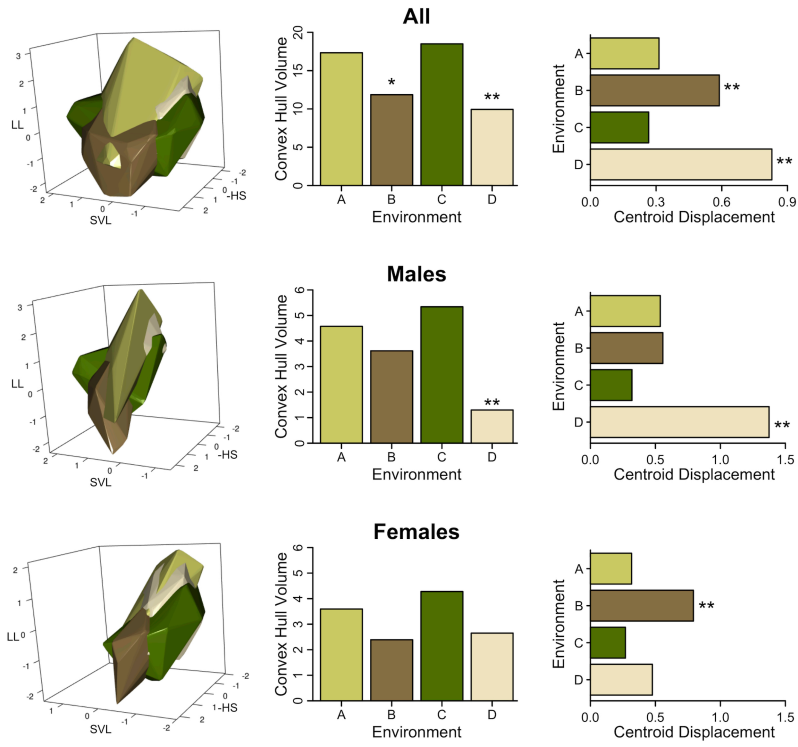
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685 Figure 5

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