1 **Narrow endemics of the Almeria Province (Andalusia, Spain) differ in their traits and**

2 **ecological niche compared to their more widespread congeners**

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Abstract Understanding the evolutionary ecology of geographically restricted species is of great importance to the design of conservation strategies and to gain insight into the evolutionary processes involved in the origin and maintenance of those species. With a very high proportion of endemic species and/or subspecies, the province of Almeria in Andalusia (SE Spain) represents a prominent hotspot of plant diversity in the Mediterranean Basin. In this paper, we use phylogenetically independent contrasts to examine whether narrow endemics (i.e., species mostly restricted to the Almeria Province, hereafter NE) have evolved a "syndrome of endemism". Based on published trait values, we test if (i) NE occupy a particular altitudinal range, possess a smaller niche breadth and occur within particular plant associations and if (ii) NE have distinct vegetative and reproductive traits. We find that, compared to their more widespread congeners, NE i) occupy a narrower altitudinal range at the upper or lower limits of their congener's range; ii) occur in a smaller number of plant communities that are distinct from the communities of widespread species; and iii) have an 11% shorter flowering duration, 28% fewer flowers per inflorescence, 30 % reduced floral display, and 23% lower floral attractiveness. These differences are not explained by a smaller size overall or a different ploidy level. NE have apparently evolved traits that promote selfing. The shift towards higher selfing rates is interpreted as a mechanism to promote reproductive assurance and to decrease gene flow from the more widespread congeners.

Keywords Endemism • Floral display • Phylogenetically independent contrast • Rarity • Selfing • Traits

Introduction

Rare species have long fascinated biologists and represent key targets of conservation policies (Kruckeberg and Rabinowitz 1985). Among rare species, endemic species represent the most original component of regional biodiversity, and some endemics, referred to as narrow (or restricted) endemics (NE), have an area of distribution that does not exceed a few square kilometres (Stebbins 1942). Whether rare species possess particular biological attributes has attracted much attention (Gaston and Kunin 1997). Theoretical expectations predict, and a number of empirical studies have confirmed, that NE occupy marginal habitats (Drury 1974; Kruckeberg and Rabinowitz 1985; Hodgson 1986; Verlaque et al. 1997; Lavergne et al. 2003, 2004), have adaptations to stressful conditions that in turn result in low competitive ability (Walck et al. 1999), have low dispersal ability (Fiedler 1987; Hanski and Gilpin 1997) and have a breeding system with more selfing (Karron 1987; Kunin and Schmida 1997; Lavergne et al. 2004). Lower genetic diversity in rare compared to common species is one of the most robust generalizations that has emerged from empirical studies (Cole 2003). Possible causes include a higher degree of selfing, low effective population size, demographic bottlenecks and adaptations to narrow ecological conditions (Kruckberg and Rabinowitz 1985).

Comparisons of functional traits between NE and widespread species have generated much data, but generalizations are often difficult to make due to methodological problems. Thus, Bevill and Louda (1999) and Murray et al. (2002) in their reviews of 38 and 54 published studies, respectively, were only able to highlight a few robust, general trends. They concluded that patterns of correlation between traits and rarity strongly depend on the phytogeographic and ecological context. Firstly, many published studies are based on only one endemic and one widespread species. Secondly, different studies have examined different traits. Thirdly and most important, studies comparing the endemic flora with the whole flora of the same region suffer from phylogenetic and ecological bias. The endemic flora often has a distinct phylogenetic

67 assemblage and is concentrated in specific habitats (Kruckeberg and Rabinowitz 1985).

68 Therefore, any trait differences between endemics and non-endemics as a whole cannot be

69 unambiguously ascribed to differences in range size.

70 Some regions have an extremely high proportion of endemics in their flora. In the

71 Mediterranean Basin, there are several such "hotspots of endemism" (Médail and Quezel 1999).

72 The flora of southern Spain has one of the highest proportions of endemics in the Mediterranean

73 Basin (553 taxa are endemic to southern Spain, i.e., 15% after Melendo et al. (2003); 480 species

74 are endemic to Andalusia after Mota et al. (2003)). In particular, endemism peaks in the Sierra

75 Nevada, which has the highest concentration of endemic species in Europe (Melendo et al. 2003).

76 Such a high proportion is explained by the high ecological heterogeneity of the region (both

77 climatic and geomorphologic) (Rivas-Martinez et al. 1997, Melendo et al. 2003) combined with its

78 relative geographical isolation since the Pleistocene (Matamala Garcia 2007). In a thorough

79 analysis of the endemic flora of southern Spain, Melendo et al. (2003) showed that the region has

80 a very distinct taxonomic assemblage and is richer in Lamiaceae, Plumbaginaceae, and

81 Brassicaceae but poorer in Poaceae and Apiaceae compared to the general flora. Biological

82 differences with the general flora are striking and include a higher proportion of chamaephytes

83 and a lower proportion of therophytes among the endemics. Entomogamy is overrepresented,

84 and anemogamy is underrepresented in the endemics compared to the non-endemics of southern

85 Spain. Most of these biological differences can be ascribed to differences in the taxonomic

86 assemblage of the endemic flora (Melendo et al. 2003). Therefore, any attempt to analyse the

87 biological traits of the endemic flora of southern Spain must correct for phylogenetic bias.

88 One possible method to overcome such bias is to use a comparative approach based on

89 phylogenetically independent contrasts (Harvey and Pagel 1991). In this approach, a contrast may

90 consist of a pair of related species, one of which is a narrow endemic and the other a widespread

91 species. Thus, the two species in a pair share a broad common genetic background and differ

92 mostly in the size of their range. Any trait differences between them may be related to the

93 contrasting size of their area of distribution. Three studies of the flora of the Mediterranean Basin

94 have used this approach. Kunin and Schmida (1997) investigated 33 pairs of species in the flora

95 of Israel and found that narrow endemics were generally less attractive to pollinators if self-

96 compatible or more attractive if self-incompatible. Lavergne et al. (2003, 2004) examined a broad

97 range of traits in 20 species pairs in Mediterranean France and found that restricted species had

98 attributes characteristic of lower competitive ability, lower reproductive output, and higher selfing

99 rates. They also tended to occupy marginal, rockier habitats. Luna and Moreno (2010)

100 investigated the regeneration niche for 53 species pairs in eastern Spain and found no significant

101 differences between the narrowly distributed and widespread species.

102   In this paper, we use phylogenetically independent contrasts to test if the NE of the flora

103 of eastern Andalusia, more specifically the Almeria Province, have distinct biological and

104 ecological traits compared to their widespread congeners. To that end, we use data from standard

105 floras. Measurements of plant height, leaf size, flower size and number, fruit and seed size, and

106 phenology are used to examine if NE are generally smaller and have distinct reproductive

107 strategies. Lower values of floral display are expected if NE have a breeding system with more

108 selfing (Goodwillie et al. 2010), and seed size and plant height are used as proxies of dispersal

109 capacity (Thompson et al. 2011). Ecological data include altitudinal range (upper and lower

110 altitudinal limits and extension) and the phytosociological units (associations) in which the species

111 occur. These data are used to compare the niches of the NE and the widespread species. In

112 particular, we address the following questions: i) Do NE occupy a narrower niche (i.e., narrower

113 altitudinal extension and fewer phytosociological units)? ii) Do NE occupy a distinct niche; i.e.,

114 do they occur in distinct plant communities not occupied by widespread species, and do they

115 occupy a distinct altitudinal range?

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Materials and methods

Phytogeographic context

The province of Almeria is geographically delimited in the E and the S by the Mediterranean Sea, in the W and NW by mountain chains oriented W-E, the Sierra Nevada, Sierra de Gador, Sierra de Los Filabres, and in the N by the Sierra de las Estancias and Sierra de María. The province is extremely diversified in terms of climate due to its broad altitudinal range. Its coastal region represents the most arid area in Europe with a mean annual rainfall of 289 mm and a mean annual temperature of 18.1°C in Almeria. In contrast, mean annual temperature is 3.8°C, and mean annual rainfall is 705 mm in the upper slopes of the Sierra Nevada. The area of this study belongs to three biogeographic sectors with different percentages of endemism: Nevadense (15.5%), Alpujarreño-Gadorense (2.5%) and Almeriense (6.6%) (Rivas-Martinez et al. 1997).

A check-list of species endemic to the Almeria Province has been established based on the Flora Iberica (Castroviejo et al. 1986-2012) and the digital Flora Vascular de Andalucia Oriental (Blanca et al. 2011). However, as basing endemism on administrative boundaries makes little sense, the list has been extended to species whose distribution extends to the Sierras in the adjoining provinces of Murcia or Granada. Widespread, congeneric species have been selected from the flora of the Almeria Province as follows. A widespread species is defined here as a species whose distribution area covers at least five provinces; a more restrictive criterion (i.e., a wider distribution range in the widespread species) would have decreased the number of pairs. Another restrictive ecological criterion has been applied; the altitudinal range of the widespread and the NE species must at least partly overlap, which ensures that the congeners do not occur in completely different ecogeographic contexts. The latter criterion excluded a few narrow endemics restricted to the upper slopes of the Sierras whose traits reflect the specific environmental filter of those alpine conditions (Penas et al. 2005). Distributional data were obtained from the

143 aforementioned floras and supplemented by the Anthos database (Aedo and Castroviejo 2009)

144 and SIVIM (www.sivim.info/sivi/).

145   For five genera, published phylogenies were used to select the most closely related

146 widespread species (*Arenaria*: Valcàrcel et al. 2006; *Centaurea*: Victor et al. 2007; *Genista*: Pardo et

147 al. 2004; *Festuca*: Torrecilla and Catalàn 2002; *Carex*: Escudero et al. 2008). For the other genera,

148 no phylogeny is available, or the published phylogenies do not include our endemic species. In

149 such cases, the widespread species were based on taxonomic relatedness (same section or

150 subsection in the genus) following Kelly et al. (1996). Finally, the congeners have been selected to

151 have the same life form, pollination mode and dispersal mechanism. These restrictive criteria aim

152 at maximizing the genetic relatedness of the congeners and reducing confounding sources of

153 variation not directly related to the extent of distribution area (Baskauf et al. 2001). By using

154 restrictive selection criteria, we deliberately focus on the more subtle ecological differences

155 between NE and widespread species compared to the broad differences in the life form spectrum

156 highlighted by Melendo et al. (2003).

157 A total of 25 species pairs fulfilling all of the selection criteria have been found. Two pairs have

158 been selected from the genus *Teucrium*, but they belong in different sections. For two genera,

159 *Verbascum* and *Helianthemum*, two widespread species were found to fulfil our criteria. In those

160 two cases, the traits of the NE were compared to the average value of the traits of the two

161 widespread congeners.

162   Due to the restrictive selection criteria, our sample might be biased towards neoendemic

163 species, i.e., recently diverged species that have close relatives in the regional flora, but

164 paleoendemic species are not a prominent component of the flora of southern Spain (Médail and

165 Diadema 2009). Most major clades of flowering plants are represented in our sample. The

166 overrepresentation of Lamiids (8 of 25 pairs) in our sample reflects the particular taxonomic

167 assemblage of the endemic flora of Andalusia (Melendo et al. 2003).

168

169   ***Traits***

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171   Species' trait values were obtained from two recent standard floras (Castroviejo et al. 1986-2012;

172   Blanca et al. 2010). No data were available for our species in the TRY database (Kattge et al.

173   2011). We aimed to sample a broad range of traits, describing the vegetative parts (leaf size, plant

174   height) and reproductive attributes (flower size and number, seed size). All of the traits that were

175   available for at least 10 species pairs have been included in our database.

176   Flora trait values are mostly reported as min-max ranges and are sometimes supplemented

177   by extreme values (e.g., height: (15-)25-35(-45) cm). All analyses have been conducted for the

178   minimum value, the maximum value, the arithmetic mean of the minimum and the maximum

179   values and the arithmetic mean of the extreme values. As the results for the different values were

180   essentially the same, only those for the arithmetic mean of the min-max range are reported.

181   Vegetative traits include plant height, leaf length (L), leaf width (w) and the L*w product as

182   a proxy of leaf area. Reproductive traits include the number of flowers per inflorescence,

183   inflorescence length, corolla and calyx length, fruit length and width, and seed length. The floral

184   display was calculated as the product of the number of flowers per inflorescence * corolla length

185   (Goodwillie et al. 2010) (petal length was substituted for corolla length for *Alyssum, Arenaria,*

186   *Brassica, Helianthemum, Potentilla, Seseli,* and *Silene*; corolla diameter for *Dianthus, Limonium,* and

187   *Ranunculus*; upper petal length for *Genista* and *Ulex*). The floras describe inflorescence size in

188   terms of either length or number of flowers, so it is not possible to obtain both inflorescence

189   length and floral display for all of the species in our sample. However, these traits capture similar

190   information (Schoen et Dubuc (1990); Goodwillie et al. (2010)). Therefore, inflorescence length

191   and floral display have been pooled into a combined variable referred to as "attractiveness" to

192   increase sample size. The duration of flowering was calculated as the number of months between

193   the earliest and the latest month of flowering as reported in the aforementioned floras. Ploidy

194   level was also obtained from the floras and from Escudero et al. (2008) for *Carex.*

195

Ecological niche

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Assuming that syntaxonomic diversity is an indicator of ecological diversity, we used

phytosociological data as surrogates for niche description (Redzic 2007). The data were obtained

from the SIVIM database (www.sivim.info/sivi/). The number of phytosociological units (plant

associations) in which a species is recorded in the province of Almeria was used as a proxy for

niche breadth. However, that number is biased by sampling effort. To correct for sampling bias,

we used a resampling method without replacement. For each species pair, if the NE is recorded

in r_{NE} relevés representing a total of a_{NE} associations and the widespread species is recorded in r_W

relevés representing a_W associations (with $r_{NE} < r_W$), the r_{NE} relevés with the widespread species

were randomly resampled 100 times, and the average of the number of associations was used as

the unbiased value. Sample size was as follows: *Alyssum* (9), *Arenaria* (104), *Carex* (70), *Centaurea*

(6), *Coris* (15), *Dianthus* (9), *Genista* (38), *Helianthemum* (8), *Herniaria* (65), *Potentilla* (16), *Ranunculus*

(13), *Sideritis* (9), *Teucrium* (21), and *Ulex* (13).

The altitudinal niche was also analysed, using the upper and lower altitudinal limits (in m

above sea level) from the abovementioned floras. Altitudinal range, a descriptor of niche breadth

(number of meters of extension), and mean altitude, a descriptor of niche location (arithmetic

mean of upper and lower altitudinal limit), have been calculated for each species.

214

Data analysis

To test the null hypothesis that NE species and their congeners have the same trait values, paired

Student t-tests were performed. When differences between species were not normally distributed

(Shapiro test), a paired Wilcoxon signed rank test was applied.

For chromosome number, the data could not be analysed in the same way because some

species had two different numbers. In such cases, the different cytotypes of the same species

221   were treated as different taxa, and new pairs were created accordingly. As this resulted in

222   pseudoreplication, a conservative test was applied, and the number of degrees of freedom in the

223   Wilcoxon test was not increased.

224   Because the analysis of individual traits resulted in many simultaneous tests and did not

225   consider correlations among traits, a multivariate analysis was also performed. Principal

226   component analysis was conducted on the correlation matrix of a subset of the 7 variables and 10

227   species pairs without missing values (corolla length, floral display, flowering duration, flower

228   number, leaf area, fruit length, and height; genera included: *Arenaria, Brassica, Chaenorhinum,*

229   *Helianthemum, Herniaria, Linaria, Potentilla, Ranunculus, Seseli,* and *Verbascum*). Ecological data were

230   not included in this analysis. The first and second principal components were then used as new

231   synthetic variables and subjected to paired t-tests. All statistical analyses were performed with R

232   (version 2.14.0) (R Development Core Team 2009).

233

234   **Results**

235

236   Of the 18 variables considered, 7 showed a statistically significant difference between NE and the

237   widespread species (i.e., altitudinal range, lower altitudinal limit, number of communities,

238   flowering duration, number of flowers, floral display, and attractiveness) (Table 2, Fig. 1).

239

Ecological traits

On average, NE had a 52% narrower altitudinal range (611 m) compared to widespread species (1515 m) (Table 2, Fig. 1a), and this difference was true for 22 of 25 species pairs. The altitudinal distribution of NE and widespread species were strikingly different (Fig. 2). Thus, NE showed a strongly bimodal distribution frequency as they were concentrated at both ends of the altitudinal gradient (0-450 m and 2400-2900 m, respectively) (Fig 2a). Widespread species had a unimodal distribution that peaked at intermediate altitude (900-1300 m) (Fig. 2b).

The number of phytosociological units was significantly lower in NE compared to widespread species, ranging from 2 to 24 in widespread species and from 1 to 13 in NE (Table 2, Fig. 1b). The number of units was equal or smaller in the NE in 14 of 15 pairs with *Herniaria* being the only exception. In seven pairs, the endemic and the widespread species did not occur in the same association. In seven other pairs, only one association was shared between the two species, and in the case of *Thymus*, four associations were shared (Fig. 3).

Reproductive traits

Flowering duration was 11% (i.e., ca. one month) shorter in NE (Table 2); the opposite trend was observed in only five pairs (Fig. 1c). The number of flowers per inflorescence was 28% lower in NE (Table 2) (i.e., lower in 7 pairs, equal in 2 pairs and higher in 1 pair (*Potentilla*)) (Fig. 1d). Floral display was 29% smaller in NE (Table 2) (Fig. 1e). NE had a higher floral display value in only two pairs, namely, *Ranunculus* and *Chaenorhinum*. For the combined "attractiveness" variable, NE had 23% lower values (Table2, Fig. 1f). NE had higher values of this trait in only three pairs (*Potentilla, Ranunculus,* and *Chaenorrhinum*). Inflorescence length was lower in the NE in four cases, equal in three cases and higher in only one of eight cases (*Teucrium* sect. *Simplicipilosa*), but the difference (10.5 cm versus 8.7 cm) was not significant (Table 2). Corolla length, calyx length, fruit length and width, and seed size were not significantly different between NE and widespread species (Table 2).

266

Vegetative traits

268 No statistically significant difference was found between NE and widespread species for

269 vegetative traits (leaf length and width, leaf area, and plant height) (Table 2).

270

Ploidy level

272 Chromosome numbers are available for 20 pairs (Table 1). In 12 pairs, the two species had the

273 same ploidy level. In seven pairs, the widespread species had several ploidy levels (two or three),

274 but this was found in only 1 NE, and the difference in the proportions (i.e., 1 of 20 vs. 7 of 20)

275 was significant (Fisher's exact test, two-sided: P=0.048). In the pairwise comparison tests, the

276 different cytotypes of the same species were treated as different taxa. For the 30 new pairs, the

277 results of the Wilcoxon signed-rank test were not significant (V=58, P=0.75 n=20).

278

Principal Component Analysis

280 PC1 and PC2 accounted for 29% and 25% of the variance, respectively. PC1 was mostly

281 correlated to leaf area, fruit length and corolla size (Fig. 4a), and it captures most of the

282 phylogenetic source of variation. Thus, genera with large flowers, large leaves and large fruits

283 (e.g., *Verbascum*) are mostly located on the left side of the scatter plot while genera with the

284 opposite combination of traits (e.g., *Herniaria*) are on the right side of PC1 (Fig. 2a). PC2 was

285 negatively correlated to floral display, flowering duration and the number of flowers per

286 inflorescence. Compared to their widespread congeners, NE had significantly higher scores on

287 PC2 (paired t-test: t = 3.17, df = 9, P = 0.011), and this was true in eight of ten pairs. In one pair,

288 there was no tendency (*Potentilla*), and in one pair, the difference was in the opposite direction

289 (*Ranunculus*). NE also had a higher score on PC1 (verified in 7 of 10 pairs), but the difference was

290 not significant (paired t-test: t = 1.92, df = 9, P = 0.086).

291

Discussion

Narrow endemics occupy narrower, marginal niches

We found that endemics have narrower altitudinal ranges than their widespread congeners. This result fits well with the general correlation between niche breadth and the extent of geographical range in plants (Slatyer et al. 2013), which was verified for endemic species in the Alps (Essl et al. 2009). That pattern is demonstrated here for the first time in a multispecies, phylogenetically controlled comparison. Much more interestingly, the altitudinal niche of endemics is not randomly nested within the niches of their widespread congeners. Endemics are strikingly more frequent at both ends of the elevational gradient in sharp contrast with the distribution of widespread species, which peak at mid-altitudes. The positive correlation between altitude and the proportion of endemics in the flora of the Sierra Nevada has recently been confirmed by Fernandez-Calzado et al. (2014). The low altitude endemics in our study are narrow endemics of the Almeriense sector (Rivas-Martinez et al. 1997). Compared to the regional climate of Andalusia, these two groups of endemics occur in extreme conditions with cooler temperatures and a shorter growing season at high altitude (oro-Mediterranean humid climate) and hot, extremely dry conditions in the region of Cabo de Gata (thermo-Mediterranean semiarid climate) (Rivas-Martinez et al. 1997). Thus, with respect to altitude and climate, narrow endemics in the Almeria Province occupy marginal niches compared to their widespread congeners.

Niches were also assessed by means of phytosociological units. The results are again clear-cut with endemics occurring in 28% fewer phytosociological units. Furthermore, they also tend to occur in distinct phytosociological units. Assuming that phytosociological diversity indicates ecological diversity (Redzic 2007), our results suggest that endemics are indeed ecologically specialised species. Taken together, the altitudinal and phytosociological distributions of endemics in this study are consistent with earlier generalisations that endemics occupy marginal

318   and/or stressful habitats (Drury 1974; Kruckeberg and Rabinowitz 1985; Lavergne et al. 2003,

319   2004; Medail & Verlaque 1997), including Baetic high mountains (Penas et al. 2005). In the flora

320   of California, the ranges of narrow endemic species are often nested within those of their more

321   widespread sister species. This suggests that narrow endemics have sympatrically diverged in a

322   process referred to as "budding speciation" (Anacker & Strauss 2014). In the Almeria Province,

323   however, the situation is somewhat different as the endemics are markedly concentrated at the

324   two extremes of an altitudinal gradient. This may indicate that narrow endemics have originated

325   by ecological speciation in peripheral populations subjected to divergent natural selection

326   (Schluter 2009).

327

328   Adaptation to extreme habitats might entail a cost in terms of decreased competitive ability in the

329   narrow endemics (Medail & Verlaque 1997; Imbert et al. 2011). However, we found no clear

330   evidence for reduced vegetative vigour or competitive ability in endemics as they did not have

331   smaller heights or smaller leaves. This contrasts with the French Mediterranean region where

332   endemics occupy marginal habitats (rocky slopes with sparse plant cover) and do have reduced

333   competitive ability compared to their widespread counterparts (Lavergne et al. 2003, 2004).

334   However, widespread species in southern France occur in much more mesic habitats, in deeper

335   soil and in dense vegetation cover. Such habitats are scarce in the Almeria Province, so the

336   contrast in ecological conditions between NE and widespread species is less striking with both

337   endemic and widespread species occurring in arid habitats with shallow soils in open,

338   unproductive communities. Endemic species may also have a restricted geographic range due to

339   low dispersal ability (Youssef et al. 2011). We found no significant difference in propagule size or

340   plant height, two predictors of dispersal capacity for species sharing the same dispersal

341   mechanisms (Fenner & Thompson 2005; Thompson et al. 2011). Therefore, lower dispersal

342   capacity is less likely to account for the much more restricted geographic range of endemics

343   compared to their congeners.

344   However, narrow endemics might still have lower reproductive output (Murray et al. 2002;

345   Lavergne et al. 2004) resulting in low propagule pressure and lower colonizing ability, but field

346   measurements are needed to test this hypothesis.

347

348   *Are endemics more prone to selfing?*

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350   Lower attractiveness to pollinators in narrow endemics is a striking result of this study.

351   Interestingly, smaller floral displays and inflorescence size are not by-products of smaller plant

352   size because plant height, leaf size and calyx size did not differ between endemics and widespread

353   species. Our results indeed suggest a breeding system with more selfing in narrow endemics.

354   Species existing as small, isolated populations or those adapted to specific habitats are more

355   prone to evolving a selfing breeding system than species with the opposite attributes (Kunin and

356   Schmida 1997; Karron 1987; Lavergne et al. 2003, 2004; Lowry and Lester 2004). Other studies

357   have also found lower attractiveness to pollinators in rare species (Kunin and Schmida 1996;

358   Lavergne et al. 2004; Rymer et al. 2005), and these findings suggest that lower attractiveness to

359   pollinators in the endemics has evolved in response to selective pressure (Charlesworth and

360   Charlesworth 1981; Goodwillie et al. 2010). The shorter flowering duration in the endemics in

361   this study is also consistent with a breeding system with more selfing (Bolmgren et al. 2003;

362   Elzinga et al. 2007; Rathcke and Lacey 1985). Shorter flowering duration in rare species was also

363   found by Murray et al. (1999), Lahti et al. (1991), Cadotte and Lovett-Doust (2002) and

364   Gabrielova et al. (2013). The elevation of self-fertilization in narrow endemics may facilitate their

365   invasion of marginal habitats by reducing the level of maladaptive gene flow from nearby

366   populations and by conferring reproductive assurance (Levin 2010). Transition to selfing may

367   itself be a driver of speciation (Wright et al. 2013), and our results are consistent with a scenario

368   of selfing endemics evolving from widespread outcrossers.

369   Pollen limitation is another selective force promoting evolution towards increased rates of

370   selfing (Knigth et al. 2005). Biodiversity hotspots are known to be prone to pollen limitation

371   (Vamosi 2006), and Alonso et al. (2010) demonstrated that transitions to endemism in hotspots

372   are generally associated with transitions to self-compatibility. Endemic species may thus be less

373   attractive to pollinators (Knigth et al. 2005) and particularly vulnerable to pollen limitation due to

374   their low population density (Brown 1984; Gaston et al. 2000), marginal habitats, or short

375   flowering duration (Cadotte and Lovett-Doust 2002 Gabrielova et al. 2013, Lahti et al. 1991,

376   Murray et al. 1999). An outcrossing breeding system may increase the risk of receiving

377   heterospecific pollen, which may be critical in endemics that exist as small populations in contact

378   with close relatives; this is indeed true in the Almeria Province (Harder et al. 1993). Therefore,

379   for autocompatible species, increased selfing is expected to evolve in narrow endemics that co-

380   occur with close relatives in biodiversity hotspots. In contrast, self-incompatible endemic species

381   cannot escape pollen limitation by selfing, so they actually evolve towards more attractive floral

382   traits (Kunin and Schmida, 1996). In our study, attractiveness was higher in the endemic in only

383   three pairs, i.e., *Ranunculus, Teucrium* and *Chaenorhinum.* Interestingly, *Ranunculus* is known to be

384   self-incompatible (Lundquist 1990).

385

386   **Conclusions**

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388   In conclusion, our comparative approach based on phylogenetically independent contrasts has

389   revealed few differences between endemics and their widespread relatives, but the differences in

390   ecology and traits are mutually consistent. Endemics of the Almeria Province appear to be

391   narrow-niched ecological specialists, and they exhibit smaller floral displays that are most likely

392   related to increased selfing. Altogether, these results are consistent with a scenario of

393   neoendemism resulting from the parapatric divergence of populations at the ecogeographical

394 margins of the range of widespread species. Field population biology and phylogeographic

395 studies are needed to test this hypothesis.

396

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Table 1 The 25 studied species pairs (the first species in a pair is the endemic species). Nomenclature follows Castroviejo *et al.* (1986-2012) and Blanca et al. (2009). Number of populations, number of individuals and occupancy area are from Bañares et al. (2010), Blanca et al. (1999, 2000), Cabezudo et al. (2005), Mota et al. (2003), and Moreno (2008). Number of chromosomes is from Castroviejo *et al.* (1986-2012), Blanca *et al.* (2009) and for the genus *Carex*, Escudero et al. (2008).

Life form: Na=nanophanerophyte, Ch=chamaephyte, He=hemicryptophyte, Ge=geophyte, Th=therophyte

Dispersal: EX=exozoochorous, MY=myrmecochorous, Ane=anemochorous, Bar=Barochorous

Pollination: Ent=Entomogamous, Ang=Anemogamous. Reproductive system: hermaphrodite except if "+ g": gynodioecious

Geographic range: Al=Almeria Province, Gr=Granada Province, sector Nevadense, Mu=Murcia Province

Family	Genus	Species	N. pop.	N. indiv.	Occupancy area (km²)	N. Chrom.	Geographic range	Life form/dispersal/pollination
Apiaceae	*Seseli*	*S. intricatum* Boiss. *S. montanum* subsp. *montanum* Willk.	5	5000	195	22 22, 33	Al W Medit Basin	He/Bar/Ent, Ane He/Bar/Ent
Asteraceae	*Centaurea*	*C. sagredoi* Blanca *C. monticola* Boiss. ex DC.	2	149	65	18 18	Al SE Spain and Morocco	He/MY/Ent He/MY/Ent
Brassicaceae	*Alyssum*	*A. gadorense* P.Küpfer *A. montanum* L.	5	124	20	 8, 18, 24	Al W Medit Basin	Ch/Bar/Ent Ch/Ane/Ent
Brassicaceae	*Brassica*	*B. repanda* subsp. *almerienses* Gomez Campo *B. repanda* subsp. *blancoana* (Boiss.) Heywood	3	331	12	20 20	Al. (Gr) E, S & SE Spain	He/Bar/Ent He/Bar/Ent
Caryophyllaceae	*Arenaria*	*A. tetraquetra subsp. amabilis* (Bory) H. Lindb *A. armerina* subsp. *armerina* Bory				40 28, 30	Al. (Gr) SE Spain	Ch/Bar/Ent Ch/Bar/Ent
Caryophyllaceae	*Dianthus*	*D. charidemi* Pau. *D. broteroi* Boiss. et Reut.	17	5000	1229	 60	Al. (Mu) S Spain	Ch/Bar/Ent Ch/Bar/Ent
Caryophyllaceae	*Herniaria*	*H. boissieri* J. Gay *H. scabrida* Boiss.	5	750	2.8	18	Al. (Gr) Spain, Portugal	Ch/Bar/Ent Ch/Bar/Ent
Caryophyllaceae	*Silene*	*S. littorea subsp. adscendens* (Lag.) Rivas Goday *S. littorea* subsp. *littorea* Brot.	22	3740	7147	 24	Al Spain, Portugal, N Afr.	Th/Bar/Ent Th/Bar/Ent
Cistaceae	*Helianthemum*	*H. alypoides* Lisa et Rivas Goday *H. hirtum* Mill. *H. violaceum* Lange	7	2000000	2045	20 20	Al W Medit Basin W Europe	Ch/Bar/Ent Ch/EX/Ent Ch/EX/Ent
Cyperaceae	*Carex*	*C. camposii* Boiss et Reut. *C. mairei* Coss. et Germ.	3	750	9	72 68, 69, 70	Al E Spain	He/Bar/Ang He/Bar/Ang
Fabaceae	*Genista*	*G. versicolor* Boiss. *G. longipes* subsp. *longipes* Pau.				36 18	Al et Gr SE Spain	Na-Ch/Bar/Ent Ch/Bar/Ent

Family	Genus	Species						
Fabaceae	*Ulex*	*U. canescens* Lange	9	3241	1150	32	Al	Na/MY/Ent
		U. parviflorus subsp. *parviflorus* Pourr.				32	Andalusia	Na/MY/Ent
Lamiaceae	*Nepeta*	*N. nepetella* subsp. *laciniata*					Al. (Gr)	Ch/Bar/Ent
		N. nepetella subsp. *murcica*				34	SE Spain and Morocco	Ch/Bar/Ent
Lamiaceae	*Sideritis*	*S. hirsuta* L.				26	W Medit Basin	Ch/Ane/Ent
		S. osteoxylla (Pau.) Alcaraz *et al.*				28, 56	Al	Ch/Ane/Ent
Lamiaceae	*Teucrium sect. Polium*	*T. hieronymi* Sennen				39	Al	Ch/EX/Ent + g
		T. capitatum L.				26, 39, 52	Spain, Portugal	Ch/EX/Ent + g
Lamiaceae	*Teucrium sect. Simplicipilosa*	*T. charidemi* Sandwith.	16	2180	4591	26	Al	Ch/EX/Ent
		T. eriocephalum Willk. subsp. *eriocephalum*				26	SE Spain	Ch/EX/Ent
Lamiaceae	*Thymus*	*Th. hyemalis* subsp. *millefloris* (Rivera et al.) R. Morales	2	828	1000	58	Al	Ch/Ane/Ent
		Th. baeticus Boiss. ex Lacaita				58	S & SE Spain	Ch/Ane/Ent
Plantaginaceae	*Chaenorhinum*	*C. grandiflorum* (Coss.) Willk. subsp. *grandiflorum*	9	-	1375		Al	Th/-/Ent
		C. minus subsp. *minus* (L.) Lange				14	Cosmop.	Th/Ane/Ent
Plantaginaceae	*Linaria*	*L. oblongifolia* subsp. *benitoi* (Fern. Casas) L.Sáez, M.B.Crespo & M.Bernal	4	4000	1000	12	Al	Th/-/Ent
		L. oblongifolia Boiss et Reut. subsp. *haenseleri*				12	S Spain & Portugal	Th/-/Ent
Plumbaginaceae	*Limonium*	*L. tabernense* Erben	10	20150	5006	16	Al	Ch/Ane/Ent
		L. cossonianum Kuntze				16	SE Spain + Balearic isl.	Ch-He/Ane/Ent
Poaceae	*Festuca*	*F. pseudoeskia* Boiss.				14	Al. (Gr)	He/Ane/Ang
		F. scariosa (Lag.) Pau				14	SE Spain	He/Ane/Ang
Primulaceae	*Coris*	*C. hispanica* Lange	12	5000	1088	18	Al	Ch/Ex/Ent
		C. monspeliensis L.				18, 56	W Medit Basin	Ch/Bar/Ent
Ranunculaceae	*Ranunculus*	*R. acetosellifolius* Boiss.	7	1950	87	16	Al. (+Gr)	Ge/EX/Ent
		R. demissus DC.				16	Cosmop. (mountains)	Ge/EX/Ent
Rosaceae	*Potentilla*	*P. nevadensis* Boiss.	8	387	14	14, 28	Al. (Gr)	He/Bar/Ent
		P. hirta L.				14	W Medit Basin	He/Bar/Ent
Scrophulariaceae	*Verbascum*	*V. charidemi* Murb.	17	223	30		Al	He/Bar/Ent
		V. simplex Labill.				32	W Medit Basin	He/-/Ent
		V. virgatum Stokes				62, 64, 66	Cosmop.	He/EX/Ent

Table 2 Comparison of traits and ecological ranges between narrow endemic (NE) and widespread (W) species in Almeria Province (SE Spain): phylogenetically independent contrasts. n=number of pairs. The magnitude of difference is calculated as the difference between the value of the endemic and the widespread species, expressed in percentage. The results are from Student's paired t-test or Wilcoxon matched-pairs signed-rank test if the data were not normally distributed.

	Student test t=	Wilcoxon test W=	n	P	NE vs. W	Magnitude of difference
Ecological range						
Altitudinal range	-3.17		25	$6\ 10^{-7}$	E < W	52%
Upper altitudinal limit	-1.77		25	0.09		
Lower altitudinal limit		17.5	25	0.00042	E > W	57%
Number of plant communities	4.17		17	0.0034	E < W	32%
Reproductive traits						
Flowering duration	2.20		24	0.038	E < W	11%
Number of flowers per inflorescence	2.71		10	0.024	E < W	28%
Inflorescence length	1.49		8	0.19		
Calyx length		57	20	0.59		
Corolla length		130	23	0.63		
Floral display	3.25		13	0.0069	E < W	29%
Attractiveness		156	21	0.0023	E < W	23%
Fruit length		123	22	0.74		
Fruit width	1.11		14	0.28		
Seed length	0.79		11	0.48		
Vegetative traits						
Height	1.58		25	0.47		
Leaf length		162	23	0.25		
Leaf width		123	23	0.81		
Leaf length x Leaf width	-0.02		22	0.99		

9   Figures

10

11   **Fig. 1** Comparison of ecological attributes and traits of endemic species of the province of

12   Almeria and widespread congeners. Each point represents a species pair. The results of paired

13   comparison tests (Student t-test or Wilcoxon test) are indicated. The first bisector represents

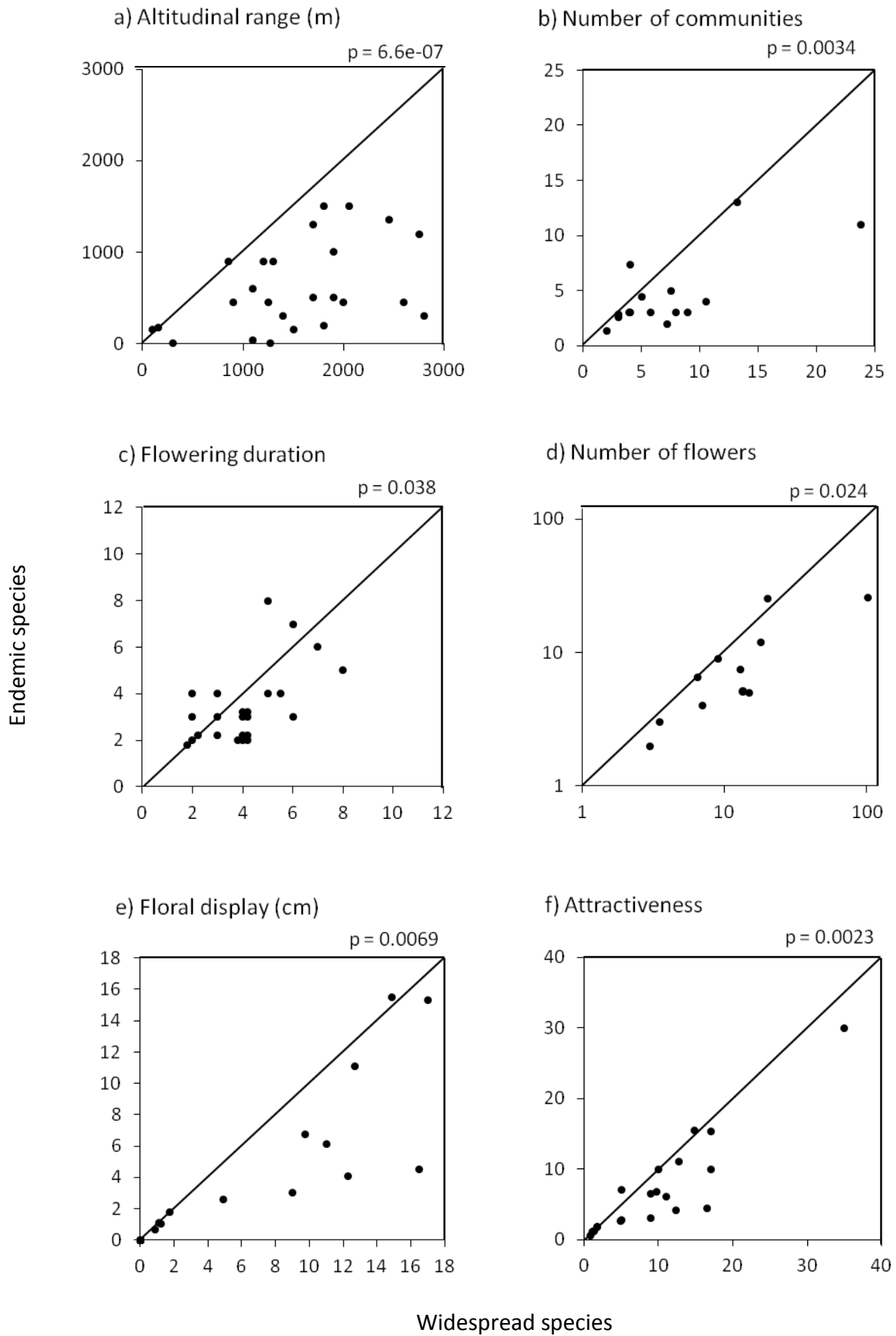14   equal trait values for endemic and widespread species.

15

16   **Fig. 2** Frequency distribution of the mean altitude of the occurrence of narrow endemic species

17   and widespread congeners in the province of Almeria.

18

19   **Fig. 3** Number of plant associations in which narrow endemic species and widespread congeners

20   occur in the province of Almeria and number of shared associations (corrected for differences in
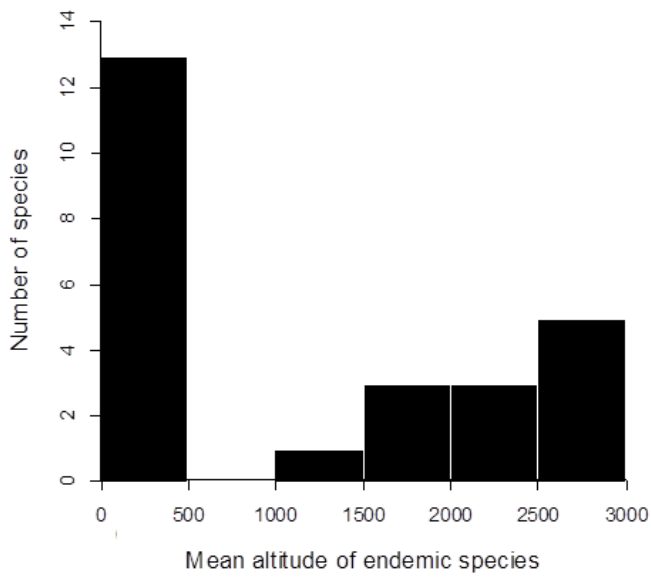
21   sample size).

22

23   **Fig. 4** Principal component analysis of seven traits in ten species pairs consisting of an endemic

24   species of the province of Almeria and a widespread congener. a) Scatterplot of species; the two

25   congeners are linked by a vector (arrow: widespread to endemic). b) Trait loadings on PC1 and

26   PC2; the red vector represents the average of the 10 species pairs. Traits included: Corolla

27   (corolla length); leaf area (leaf length x leaf width), Fruit (fruit length), Height (vegetative height),

28   Flo_disp (floral display), Flo_dur (flowering duration), Flo_nb (flower number); Genera included

29   (widespread-endemic): *Seseli* (1-2), *Herniaria* (3-4), *Arenaria* (5-6), *Ranunculus* (7-8), *Potentilla* (9-10),

30   *Chaenorhinum* (11-12), *Verbascum* (13-14), *Linaria* (15-16), *Helianthemum* (17-18), *Brassica* (19-20).
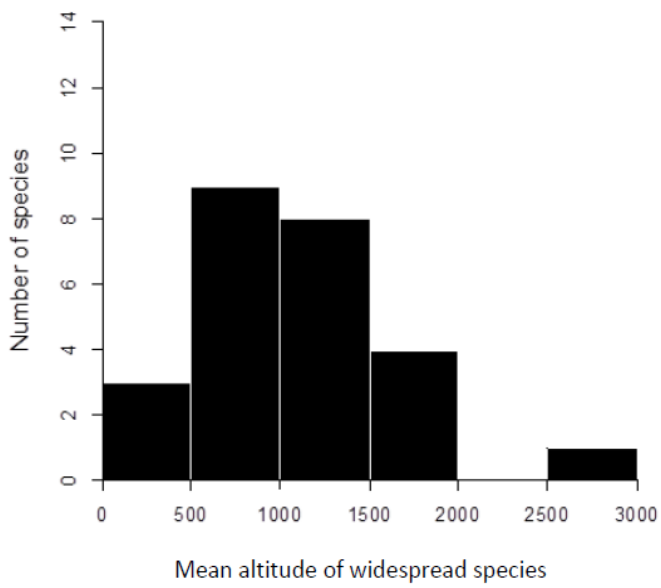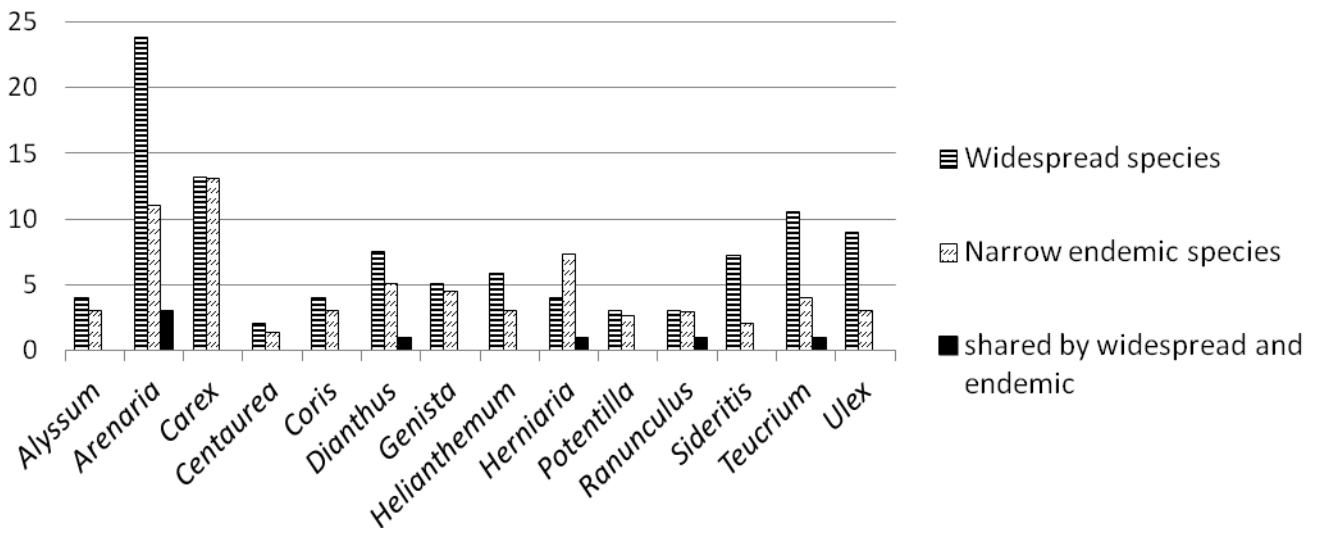
a) Altitudinal range (m) p = 6.6e-07

b) Number of communities p = 0.0034

c) Flowering duration p = 0.038

d) Number of flowers p = 0.024

e) Floral display (cm) p = 0.0069

f) Attractiveness p = 0.0023

Endemic species

Widespread species

32   Figure 2

33

Mean altitude of endemic species

34

Mean altitude of widespread species

35   Figure 3

36

37

38

39   Figure 4

40

41