

Ecological niche differentiation in peripheral populations: a comparative analysis of eleven Mediterranean plant species

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1 **Ecological niche differentiation in peripheral populations: a comparative**  
2 **analysis of eleven Mediterranean plant species**

3

4 Papuga G.<sup>1,2,3</sup>, Gauthier P.<sup>2</sup>, Pons V.<sup>2</sup>, Farris E.<sup>1</sup>, & Thompson J.D.<sup>2</sup>

5 1. Dipartimento di Scienze della Natura e del Territorio, Università degli Studi di Sassari, via  
6 Piandanna, 4, 07100 Sassari, Italy

7 2. UMR 5175 CEFE, CNRS, 1919 route de Mende, 34293 Montpellier cedex 5, France

8 3. Conservatoire Botanique National Méditerranéen de Porquerolles, antenne Languedoc-  
9 Roussillon, parc scientifique Agropolis-B7, 2214 boulevard de la Lironde, 34980 Montferrier  
10 sur Lez, France

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14 Author for correspondence: Guillaume Papuga

15 Email: guillaume.papuga@gmail.com

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19 **Abstract**

20 **Aim:** The “central-peripheral” hypothesis has provided a baseline for many studies of  
21 population dynamics and genetic variability at species distribution limits. Although  
22 peripheral populations are often assumed to occur in ecologically marginal conditions, little  
23 is known about whether they effectively occur in a distinct ecological niche.

24 **Location:** Western Mediterranean basin

25 **Time Period:** 2013-2014

26 **Major taxa studied:** A cross-taxa analysis of 11 Mediterranean vascular plants.

27 **Methods:** We quantified variation in the ecological niche between populations at the  
28 northern range limits of species in Mediterranean France and those in the central part of the  
29 distribution in continental Spain or Italy. We analyzed both the macro-ecological niche  
30 where populations occur in terms of broad habitat and altitudinal range and the micro-  
31 ecological niche where individual plants grow in terms of soil and structural biotic and  
32 abiotic characteristics.

33 **Results:** Most species occur in a single broad habitat type common to central and peripheral  
34 populations and have a narrower altitudinal range in the latter. In contrast, for the micro-  
35 ecological niche we detected marked variation in several niche parameters among central  
36 and peripheral populations. Although many differences are species-specific some are  
37 common to several species. We found a trend towards narrower micro-niche breadth in  
38 peripheral populations.

39 **Main conclusions:** Our results illustrate the importance of studying the precise ecological  
40 characteristics where plants grow and the pertinence of a multi-species approach to  
41 correctly assess niche variation. The ecological originality of peripheral populations  
42 underlines their evolutionary potential and conservation significance.

## 43 Introduction

44           The idea that populations close to species' range limits may show fundamental  
45 differences when compared with those in the central part of their distribution is a  
46 fundamental tenet in ecology and biogeography (Sagarin & Gaines, 2002; Eckert *et al.*, 2008;  
47 Sexton *et al.*, 2009; Pironon *et al.*, 2016). The exploration of this so-called "central-  
48 peripheral" hypothesis has concerned three main themes. First, patterns of population and  
49 individual abundance across a species range have led to the proposition of an "abundant  
50 center" hypothesis (Hengeveld & Haeck, 1982; Brown, 1984) that is the subject of ongoing  
51 examination (Sagarin *et al.*, 2006). Second, individual fitness and population demography  
52 have been proposed to decline towards range limits (Herlihy & Eckert, 2005; Angert, 2006;  
53 Villellas *et al.*, 2013; Abeli *et al.*, 2014), although empirical evidence remains rare (Pironon *et*  
54 *al.*, 2016). Third, many studies document lower levels of genetic variability within  
55 populations and increased differentiation among populations at range limits (Eckert *et al.*,  
56 2008). Empirical tests of the central-peripheral hypothesis have also often assumed the  
57 ecological marginality of peripheral populations, although there has been much debate  
58 concerning this issue (Soulé, 1973; Hardie & Hutchings, 2010; Pironon *et al.*, 2015). Indeed,  
59 the possibility of ecological niche differences between peripheral and central populations  
60 has received less empirical attention than the above-mentioned topics (Pironon *et al.*, 2016).

61           In plants, the diversity of environmental factors involved and the complexity of their  
62 interactions render the delimitation of a species niche a delicate issue (Pulliam, 2000). Many  
63 recent studies have focused on the climatic niche (Diniz-Filho *et al.*, 2009; Lira-Noriega &  
64 Manthey, 2014), however this provides only limited insights into our understanding of how  
65 fine-scaled population processes may vary at range limits (Curtis *et al.*, 2016). In fact, broad

66 habitat units or vegetation types do not provide the correct scale on which to identify the  
67 precise ecological niche of plants (Hall *et al.*, 1997; Miller & Hobbs, 2007), which requires  
68 explicit descriptions of the suite of resources and environmental conditions that permit plant  
69 establishment, growth and reproduction. The sessile life form of plants reinforces this need  
70 to identify the niche where plants grow because of the potential effect of highly localised  
71 ecological variation on plant performance (Chapin *et al.*, 1987; Lönn & Prentice, 2002;  
72 Jusaitis, 2005). Empirical comparison of the ecological niche of plants in central and  
73 peripheral populations have revealed differences for individual species, but no clear general  
74 pattern, be it for abiotic factors (Farris & Schaal, 1983; Duffy *et al.*, 2009; Leuschner *et al.*,  
75 2009; Wagner *et al.*, 2011), competition and community composition (Carter & Prince, 1985;  
76 Alexander *et al.*, 2007) or biotic interactions (Bruehlheide & Scheidel, 1999; Castilla *et al.*,  
77 2013).

78         A particularly interesting situation for the study of ecological differentiation in central  
79 and peripheral populations concerns the flora of southern France where many western  
80 Mediterranean species occur at their northern range limits (Jahandiez, 1937; Quézel &  
81 Médail, 2003; Noble & Diadema, 2011; Papuga *et al.*, 2015), often in peripheral isolates  
82 (Médail *et al.*, 2002; Lhotte *et al.*, 2014). These patterns are closely associated with the  
83 geological and climatic history of the region (Thompson, 2005; López de Heredia *et al.*, 2007;  
84 Médail & Diadema, 2009; Feliner, 2014). Based on a comparative analysis of 11 such species,  
85 the objectives of this paper are threefold. First, we test whether species show differences in  
86 their macro- and/or micro-ecological niche among central (in continental Spain or Italy) and  
87 peripheral (northern range limits in Mediterranean France) populations. Second, we attempt  
88 to identify whether species share similar patterns of ecological niche variation across their

89 range. Third, we test whether ecological niche breadth is different among peripheral  
90 populations compared to among populations in the central part of the distribution.

91

## 92 **Material and methods**

### 93 *Species and population selection*

94 In order to select species for a comparative analysis of niche variation among central  
95 and peripheral populations we followed a step-by-step procedure. First, we compiled a list of  
96 the 335 Mediterranean plant species (Appendix S1) that are listed for protection in France  
97 and present in the region or classified as “endangered” in the Red List of Flora of Provence  
98 (Noble *et al.*, 2015). We based our selection on listed species because their distribution is  
99 solidly documented (which is not always the case for common species) and also because of  
100 their conservation significance. We immediately excluded from this list species whose  
101 distribution in Mediterranean France is directly linked to recent human activities (e.g.  
102 species of horticultural importance such as *Chamaerops humilis* L.) and species of trees,  
103 ferns, helophytes and aquatic plants whose study would require markedly different sampling  
104 methods. We also excluded species whose taxonomic rank is under discussion or which are  
105 genetically heterogeneous (e.g. polyploid complexes). This selection reduced the list to 180  
106 species.

107 We then restricted the list to species that exhibit a clear central-peripheral type of  
108 distribution, with a central part of their range in the Iberian or Italian peninsula and/or North  
109 Africa and northern peripheral populations in the Mediterranean climate region of France.  
110 To remain in the list species were then required to have at least five known populations in

111 our database for this region (in order to make a multi-site study of variability of the  
112 ecological niche in these peripheral populations). We also excluded species for which  
113 populations in the central part of the distribution were very scattered and rare, making  
114 population localization extremely difficult. This produced a list of 39 species. We then  
115 randomly selected one species per family, except for the *Asteraceae* for which three species,  
116 each in a different clade, were selected. We included one common non-listed species,  
117 *Narcissus dubius*, which was the subject of a previous study and for which we had previously  
118 analysed a similar dataset (Papuga *et al.*, 2015). A final list of 11 species (Tab. 1, Fig. 1)  
119 containing three therophyte species, three hemicryptophytes, three geophytes, and two  
120 chamaephytes was obtained.

121 In order to select study populations for the 11 species, a geolocalized database of  
122 known population locations was compiled from four main sources: the *SILENE* database of  
123 the Conservatoire Botanique National Méditerranéen de Porquerolles (France); the *IPE*  
124 database of the Instituto Pirenaico de Ecología (Jaca, Spain); the *Biodiversidad Valenciana*  
125 data base of Valence community (Spain), and the Spanish *Anthos* online database  
126 (<http://www.anthos.es/>). We also gathered personal data from colleagues in France, Spain  
127 and Italy. Only data with a resolution of  $< 1\text{km}^2$  were used in our study (Appendix S2).

128 To compare central and peripheral populations of each species, we randomly chose  
129 five central and five peripheral populations in our database for study (Appendix S3). If a  
130 population could not be found in the field, we selected the closest known population for  
131 study. In southern France, populations were selected to cover the distribution range of the  
132 species to the west and east of the Rhône valley. Obviously, for peripheral populations the

133 distance among populations is limited, and for nine species the mean and maximum distance  
134 among peripheral populations are less than those for central populations (Tab. 1).

### 135 *Field and database examination of the macro niche*

136 For each population, the natural habitat was described in terms of vegetation  
137 structure (e.g. forest, grassland, etc.), dominant species, topographical characteristics (e.g.  
138 crest, plain, slope, etc.) and type of substrate (e.g. calcareous, granitic, quaternary soil, etc.).  
139 Based on these field descriptions and notes, we assigned each population to a broad habitat  
140 type following the EUNIS classification (<http://eunis.eea.europa.eu/habitats.jsp>). Based on  
141 information in the above databases we identified the “minimum” and “maximum” altitude  
142 values and the two limits which enclose 90% of altitude values (such that 5% of values fall  
143 below the “lower limit” and 5% above the “higher limit”) in the central and peripheral parts  
144 of the range of each species. We verified the results by comparing them with published data  
145 in *Flora Iberica* (Castroviejo, 1986).

### 146 *Field investigation of fine-scaled niche characteristics*

147 Once a population was located in the field, fine-scaled ecological characteristics were  
148 studied in three quadrats per population. Each measured either 1m<sup>2</sup> or 4m<sup>2</sup> depending on  
149 the size of individuals and its distribution pattern, and established at least 5m apart in a  
150 randomly selected high-density patch (following Lavergne *et al.*, 2004; Tab. 1). For each  
151 quadrat, we measured the slope, and visually estimated the mean height of each vegetation  
152 stratum (following Raunkiaer, 1934).

153 The ecological characteristics of each quadrat were determined with point contact  
154 data for 100 contact points (10\*10cm grid for 1m<sup>2</sup> quadrats; 20\*20cm grid for 4m<sup>2</sup> quadrats)



155 with the following elements: bedrock, blocks (>25cm), stones (2.5 – 25 cm), gravel (0.5 – 2.5  
156 cm), bare soil, lichen, moss, herbaceous and woody litter, and living plants. Each contacted  
157 plant species was identified. When several components were touched at a given point, we  
158 constrained the value of the contact point to 1, so that the total cover per quadrat could not  
159 exceed 100%. For each quadrat we calculated species richness (the number of “contacted”  
160 species), the cover of each biological type (Raunkiaer, 1934) and the Hill number associated  
161 with the Shannon diversity index (Jost, 2006) for the whole community and per biological  
162 type.

163 Field studies and experimental laboratory analyses were conducted during spring and  
164 autumn 2013 and in spring 2014. For each species central and peripheral populations were  
165 studied in the same year, roughly 2-3 weeks apart depending on population phenology.

### 166 *Soil analysis*

167 We collected one soil sample per quadrat. Soils were dried at 40°C for 48h, sieved at  
168 2mm and stored in a cool room prior to analysis. Conductivity (c) and pH (pH) were  
169 measured using an *Eutech Cyberscan*. After mixing 10g of dry soil with 20ml of water, we  
170 blended the solution during 20min, then separated phases using a centrifuge (10 minutes),  
171 and measured values in the supernatant at room temperature (circa 20°C). Water retention  
172 potential (WRP) is the percentage of water lost after drying a wet soil for 48h at 40°. Water  
173 retention capacity (WRC) was then calculated as the percentage of water remaining in this  
174 previously 40°C-dried soil by a repeated drying of the sample at 110°C for 5 hours. Organic  
175 matter (OM) was estimated as the percentage of matter lost after burning a dried sample at  
176 500°C during 5 hours. Soil samples from central and peripheral populations of a given  
177 species were analyzed at the same time.

178 *Statistical analyses*

179 Principal Component Analysis (PCA) was performed to identify correlated  
180 (redundant) measures, which were removed from further analyses (results not shown).  
181 Following this, we tested for differences among mean values for central and peripheral  
182 populations within each species with a Welch two-sample *t* test (two-sided). We also  
183 investigated differences between the two geographic groups of populations in terms of  
184 variation among their populations (niche breadth in a given region), and ran Ansari-Bradley  
185 tests to analyze levels of variation among paired samples (two-sided). Both tests were  
186 chosen for their robustness to non-normal distribution patterns.

187 Following this, to provide a comparative analysis, we plotted the mean value ( $\pm$  standard  
188 error) of each species for each ecological variable in central and peripheral populations in  
189 relation to a bisector that represents a line of equality for central or peripheral populations  
190 (following Lavergne *et al.*, 2004). Deviation from the bisector represents a difference  
191 between the two sets of populations. To statistically test this relationship we fitted a general  
192 mixed effect model, with the trait value as a response variable and species and population as  
193 random factors with population nested within species, and geographic location as a fixed  
194 factor. We carried out analysis of deviance based on type-2 Wald Chi-square tests for each  
195 analysis (Nelder & Baker, 1972).

196 To compare niche breadth of central and peripheral populations of each species we  
197 calculated niche volumes independently for central and peripheral populations using a  
198 Principal Component Analysis (PCA) on the complete set of micro-ecological niche variables.  
199 We plotted the first two axes of the PCA for each species, drew two convex hulls including all  
200 central and all peripheral populations, and calculated their surface (Broennimann *et al.*,

201 2012) (see Appendix S4 for plots). We repeated this procedure three times on subsets of the  
202 total dataset, retaining only variables of soil, abiotic and biotic compartment, to refine  
203 overall trends. We plotted each series following the procedure described above. To assess  
204 the significance of each trend, we ran single-tailed Wilcoxon sign rank tests for pairwise data  
205 with the “greater” option to test whether the niche volume is greater in the center of the  
206 range.

207 To statistically test for cross-taxa differences in the mean altitude between central  
208 and peripheral populations, we fitted a linear mixed effect model with geographic location  
209 as a fixed factor, and species as a random factor. We also plotted the mean and the  
210 maximum altitude (which includes 95% of known locations) following the procedure  
211 described above.

212 All statistical analyses were performed using R:3.2.1 (R development Core Team,  
213 2010). We corrected  $p$ -values following the Benjamini-Hochberg false discovery rate method  
214 (Benjamini & Hochberg, 1995). We present  $p$ -values that fall between 0.05 and the corrected  
215 value as weakly significant (\*) and those that are less than the corrected threshold as highly  
216 significant (\*\*).

217 To test for any spatial autocorrelation in the micro niche dataset we calculated  
218 Moran’s I index for each micro niche parameter for each species. This index varies between -  
219 1 (perfect dispersion) and 1 (perfect spatial correlation), with 0 meaning that no spatial  
220 structure can be depicted. Statistical tests associated with Moran’s I failed to depict any  
221 significant spatial autocorrelation (Annexe S7).

222

## 223 **Results**

### 224 *Macro niche*

225           For ten of the eleven species, the broad habitat (vegetation) type of central and  
226 peripheral populations was very similar (Tab. 2). Six species only occurred in one habitat type  
227 that was common to both central and peripheral populations (species codes 1, 2, 3, 4, 6, 7),  
228 one species (code 10) in two habitats both common to the two groups of populations, one  
229 species (code 5) in two habitats with one common habitat and two species (codes 9 and 11)  
230 in three habitats with two of them common to both groups. One species (code 8) occurred in  
231 four habitats in central populations and two habitats in peripheral populations. Nine of the  
232 eleven species occur in some form of Mediterranean xeric grasslands on calcareous soils  
233 (EUNIS code E1.31). Three species (codes 2, 9, 11) occur primarily on rocky outcrops. One  
234 species (code 4) occurred on restored land and in post-agricultural fields on a more acidic  
235 substrate.

236           The minimum altitude and the lower limit of altitudinal distribution for 90% of all  
237 values of peripheral and central populations were close to sea level (Tab. 3). However,  
238 species were consistently found at higher mean altitude in their central range (analysis of  
239 deviation,  $\chi^2 = 711$ ,  $df = 1$ ,  $p < 0.001$ ), with an altitudinal range ratio of central to peripheral  
240 populations that varied from 1.5 to 5 (Tab. 3, fig. 2). This ratio is exceptionally high for  
241 *Merendera filifolia* due to its restricted altitudinal amplitude in France, that contrasts with  
242 southern Spain where it occurs from sea level to >1130 m.

### 243 *Fine-scaled niche characteristics*

244 Preliminary inspection of the quadrat data showed correlated variation among some  
245 variables and very low frequencies of contact for some others. Prior to analyses we thus  
246 removed or regrouped these variables. Organic matter content and water retention  
247 potential, due to their close correlation with water retention capacity, were removed from  
248 the analysis. Block and bedrock both had consistently very low values and were thus  
249 summed into a single (“rock”) variable. Likewise, point cover data for lichens and mosses  
250 were summed into a single “cryptogam” cover variable and chamaephytes and  
251 phanerophytes into a single “woody species” cover variable. Number of species and the Hill  
252 number associated with the Shannon diversity index were strongly correlated, so we deleted  
253 the former variable due to its sensibility to rare species presence (Jost, 2006).

254 The comparison of central and peripheral populations for each species showed  
255 significant differences for between five and ten of the 20 of the analyzed ecological variables  
256 per species (Tab. 4). On average, eight variables per species showed significant variation  
257 between central and peripheral populations. Seven ecological variables (mostly biotic)  
258 showed very little variation, with no more than two species showing significant differences  
259 per variable. On average, soil characteristics and abiotic cover variables (other than bare soil)  
260 showed more significant differences (five to eight species) than biotic variables. All species  
261 showed at least one significant difference for soil characteristics and abiotic cover variables  
262 (Tab. 4). The total diversity of associated species and therophyte diversity showed significant  
263 differences for seven and six species respectively, as did total biotic cover and therophyte  
264 cover, but only for four species. Despite the large number (5-10 traits) of observed  
265 significant differences for each species (Tab. 4), only *Convolvulus lanuginosus*, *Hyoseris*  
266 *scabra*, *Merendera filifolia* and *Viola arborescens* showed common differences for a range

267 (5-6) of niche parameters. The number of traits with common differences for the other  
268 species was <5.

269 Visual inspection revealed that some variables showed a consistent pattern of  
270 differences between central and peripheral populations (Fig. 3). For soil characteristics,  
271 there was a marked overall trend for species to occur on soils with low conductivity (Fig. 3a)  
272 and a more basic pH (Fig. 3b) in peripheral populations. For abiotic niche elements, there  
273 was a cross taxa trend of occurrence on less rocky but more stony habitats in peripheral  
274 populations (Fig. 3c and 3d), with the exception of two species (*Atractylis cancellata* and  
275 *Chiliadenus glutinosus*) that showed the opposite pattern (Tab. 4). Slope did not show a  
276 general trend across species, despite the fact that seven species showed differences  
277 between central and peripheral populations (Tab. 4). For biotic niche components, total  
278 biotic cover was very similar in central and peripheral populations (Tab. 4 & Fig. 3e). Total  
279 species diversity, as quantified by the Hill number associated with Shannon's diversity index,  
280 showed a weakly significant cross taxa trend towards more diverse communities in  
281 peripheral populations (Fig. 3f). This trend is highly significant for the diversity of  
282 therophytes (six of the eleven species: Fig. 3g). The diversity of geophytes showed only a  
283 weak cross-taxa trend for three species towards higher diversity in central populations (Fig.  
284 3h). Woody and hemicryptophyte species diversity showed no patterns of variation among  
285 populations of the 11 study species.

286 Comparison of ecological variability among central and among peripheral populations  
287 (niche breadth) showed weakly significant differences (44 of the 220 tests; Tab. 5). The  
288 number of species with a significantly different niche breadth for a given trait was never  
289 more than four species, hence cross-taxa comparisons showed no significant overall trend

290 for particular variables. Notwithstanding, six species showed several traits with higher levels  
291 of variation among central populations, three species had a small number of trait differences  
292 and mostly higher variability among peripheral populations and two species showed  
293 variation for a single variable (Tab. 5). This resulted in a significant overall trend (Wilcoxon  
294 test,  $v = 55$ ,  $p = 0.0269$ ,  $p$ -corrected = 0.0537) towards smaller niche volume for peripheral  
295 populations (Fig. 4a), with only the three therophyte species that showed a significant  
296 opposite trend. When we did these analyses using the method proposed by Ben Blonder et  
297 al (date ???) we found a very similar result: most species showed a trend for wider niche  
298 breadth in central populations, but not all of them. Also, as a result of large amounts of  
299 variability in levels of variation among species (up to four orders of magnitude) the trends  
300 were not significant (annex S5). For soil characteristics (Fig. 4b) we found a cross taxa trend  
301 towards a significantly wider niche in the central part of the distribution (Wilcoxon test,  $v =$   
302  $57$ ,  $p = 0.016$ ,  $p$ -corrected = 0.054), while biotic (Fig. 4c) and abiotic (Fig. 4d) niche  
303 components showed no significant trend (Wilcoxon test,  $v = 51$ ,  $p > 0.05$  and Wilcoxon test,  $v$   
304 = 46,  $p > 0.1$ , respectively).

305

## 306 Discussion

307 This comparative study of 11 plant species shows that although central and  
308 peripheral populations occur in similar broad habitat types and across a broadly similar  
309 Mediterranean type climatic regime, their fine-scaled ecological niche parameters show  
310 marked differences between central and peripheral populations. The latter tend to occur in a  
311 less variable fine-scaled ecological niche. The precise differences are mostly species-specific,  
312 but reveal several common patterns, illustrating the pertinence of a multi-species study. The

313 fine-scaled ecological niche variation that we detect for several species in peripheral  
314 populations provides fascinating insights into the nature of ecological diversification at range  
315 limits and how we should pay careful attention to the precise location of plants and the  
316 ecological conditions of sites where individuals grow in the elaboration of translocation  
317 programs for rare species.

### 318 Ecological originality of peripheral populations

319 Our results illustrate that the broad habitat type in which populations occur is  
320 relatively similar across the range of the different species. Six out of eleven species occur in  
321 the same or very similar broad habitat types that are common to central and peripheral  
322 populations. In addition, both central and peripheral populations occur in a similar climatic  
323 regime across their range, *i.e.* in a Mediterranean-type climate with a prolonged ( $\geq 2$   
324 consecutive months) summer drought. The only difference between central and peripheral  
325 populations here is the occurrence of shorter summer-drought period and slightly cooler  
326 mean average temperatures in peripheral populations (Papuga *et al.*, 2015).

327 In direct contrast, significant variation in the micro-ecological niche between central  
328 and peripheral populations was found for between five and ten of the 20 variables (on  
329 average eight ecological variables per species) and all the studied ecological variables exhibit  
330 significant differences for at least one species (Appendix S5 for complementary analysis). Soil  
331 characteristics and abiotic cover variables showed the highest number of significant  
332 differences between central and peripheral populations, while biotic cover variables were  
333 less variable. Despite overall broad habitat similarity, the study species thus show marked  
334 ecological originality in terms of their precise ecological niche in peripheral populations. This  
335 result illustrates very clearly the importance of making explicit descriptions of fine-scale



336 environmental conditions where plants grow, instead of simply identifying local climatic  
337 conditions and broad habitat types, if we are to correctly identify the ecological niche of  
338 plant species (Hall *et al.*, 1997; Jusaitis, 2005; Miller & Hobbs, 2007). La difference de la  
339 macroniche n'impacte pas la micro (Appendix S6)

340         Although many differences are species-specific, several trends are shared across  
341 species. Three groups of species that exhibit comparable niche shifts can be distinguished.  
342 The first group is composed of seven semi-open, rocky, grassland species: *Atractylis*  
343 *cancellata*, *Convolvulus lanuginosus*, *Hyoseris scabra*, *Merendera filifolia*, *Narcissus dubius*,  
344 *Polygala rupestris* and *Viola arborescens*. Despite differences among these species in  
345 particular ecological features of their niche, they all grow in habitats with a vegetation cover  
346 ranging from 35 to 50% and illustrate a shift (clearly visible in the perennial *Convolvulus*  
347 *lanuginosus*, *Polygala rupestris* and *Viola arborescens*), from steep, rocky habitats in central  
348 populations to more stony, semi-open grassland with lower soil conductivity in peripheral  
349 populations. According to the the classical view, glacial relict populations have often  
350 persisted in rocky outcrops, cliffs and sheltered gorges (Valero-Garcés *et al.*, 2000; Médail &  
351 Diadema, 2009; Martinell *et al.*, 2010), which correspond to the ecology of central  
352 populations for the species studied here. If this was the case, then the central populations  
353 we studied would have been those that persisted in glacial refugia, which have later  
354 colonized less chasmophytic habitats during interglacial periods and since the last glaciation.  
355 However, there is evidence that the areas where we studied peripheral populations in  
356 Mediterranean France may have served as refugia during glaciation (see below). A second  
357 group of three species (*Dorycnopsis gerardi*, *Ophrys bombyliflora* and *Stipa capensis*)  
358 occurred in habitat with a high vegetation cover, on soils with a lower mineral content in  
359 peripheral populations. These species showed no variation in the macro-niche. Finally,

360 *Chiliadenus glutinosus*, the only chasmophytic species in our study, exhibits a niche shift in  
361 northern peripheral populations to steeper cliffs, with less vegetation, higher rock cover, and  
362 on soils with a higher water retention capacity in peripheral populations, the opposite trend  
363 to species in group 1.

364 In terms of the biotic micro-niche, we detected a significant cross-taxa trend towards  
365 the occurrence of species in more diverse communities (in particular the diversity of annual  
366 plants) in the peripheral part of their range. This trend is also observed in terms of the total  
367 species richness per quadrat assessed with the contact point method. It is possible that local  
368 climatic conditions may influence this result; peripheral populations occur in a less xeric  
369 Mediterranean-type climate than do most of the central populations (*e.g.* Papuga *et al.*,  
370 2015). This may determine higher species diversity in peripheral locations.

371 Finally, we detected an overall trend towards a reduction of niche breadth in the  
372 periphery of the range. Although this could have resulted from the fact that there are  
373 shorter distances between sampled populations at the periphery of a species range, micro-  
374 environmental variables exhibited little (if any) spatial structure and thus the reduction in  
375 niche breadth is unlikely to be the result of spatial autocorrelation alone (Dormann *et al.*,  
376 2007) (Appendix S7). For the broad habitat niche, there was a clear trend towards lower  
377 variability in the altitudinal amplitude of species in the peripheral part of their range. For the  
378 micro-ecological niche, soil parameters showed the most notable change in variability, with  
379 a clear shift towards soils exhibiting less variability in conductivity among peripheral  
380 populations.

381 We cannot fully discriminate the reasons underlying the patterns of niche variation  
382 between central and peripheral populations. This variation may be associated with a range

383 of factors including stabilizing selection in peripheral populations (Devictor *et al.*, 2010),  
384 dispersal limitation (Eriksson & Ehrlén, 1992; Baack *et al.*, 2006) due to a low number of  
385 propagules (Holt & Keitt, 2000), or a truncated realized niche due to a lack of equivalent  
386 ecological conditions in the central or peripheral parts of the range could artificially create  
387 the observed differences. To obtain information on the latter possibility we ran a single PCA  
388 using the ecological parameters collected in the quadrat study for four species that all occur  
389 in an identical broad habitat (E1.31, west Mediterranean xeric grassland) in both the central  
390 and peripheral parts of their range. For each species we plotted the ecological data for the  
391 two major axes for all the populations of the four species and identified the niche volume  
392 (by depicting convex hulls for their particular sites) for central (red) and peripheral (blue)  
393 populations (Fig S8). For a target species, the part of the red convex hull that does not  
394 overlap with the blue equivalent has blue crosses within it or on its immediate perimeter.  
395 These blue crosses are sites in the peripheral part of the distribution with similar ecological  
396 conditions to central populations but which are unoccupied in the peripheral part of the  
397 range. Hence the ecological conditions of central populations that are different to those of  
398 peripheral populations do occur in the peripheral part of the range, but are simply  
399 unoccupied by the target species. Hence, although there may still be a reduction in habitat  
400 availability, our results of niche differentiation between central and peripheral are not just a  
401 result of niche truncation due to habitat unavailability in the different parts of the species'  
402 range.

403         Dispersal limitation occurs in some narrow endemic species in the Mediterranean  
404 flora for which dispersal limitation and past isolation events explain distribution patterns  
405 (Youssef *et al.*, 2011). Such limitation may play a more important role than currently  
406 documented for population limitation at range limits in the northern Mediterranean. While

407 this study highlights effective changes in ecological conditions *in natura* and on a very fine-  
408 scale, the response of the taxa can be diverse, both in terms of divergence and individual  
409 plasticity.

#### 410 Ecological differentiation and species divergence

411 The patterns of ecological differentiation between central and peripheral populations  
412 detected for 11 Mediterranean plant species are of particular interest in terms of the  
413 divergence and speciation of Mediterranean endemic plants. For the California Floristic  
414 Province, Anacker & Strauss (2014) provide evidence that species divergence may often be  
415 associated with a widespread progenitor that gives rise to a restricted endemic derivative by  
416 a process of ‘budding’ speciation. This mechanism is facilitated by the occurrence of the  
417 progenitor in peripherally isolated populations that occur in ecologically different conditions.  
418 An immediate consequence of such divergence is a marked range asymmetry between  
419 progenitor and derivative species (Crawford, 2010). This range asymmetry among sister  
420 species is typical in the Mediterranean flora (Favarger & Contadriopoulos, 1961; Lavergne *et*  
421 *al.*, 2004; Martinell *et al.*, 2010). In addition, many endemic plant species in the  
422 Mediterranean flora show ecological differentiation from their proposed progenitor taxa  
423 (Lumaret *et al.*, 1987; Petit & Thompson, 1998; Debussche & Thompson, 2003; Lavergne *et*  
424 *al.*, 2004). Therefore, ecological speciation at range limits may contribute to the prevalence  
425 of narrow endemism in the Mediterranean basin, where more traditional hypotheses based  
426 on allopatric differentiation have often been brought to the fore (reviewed by Thompson,  
427 2005).

428 Our study thus provides support for the idea (Fréville *et al.*, 1998; Thompson, 1999;  
429 Crawford, 2010) that widespread species with disjunct distributions and peripheral isolates

430 such as our study species may set the scene for diversification. As Crawford (2010) argued,  
431 already differentiated sister species offer limited promise for exploring the processes that  
432 produced them. In contrast, our 11 species represent potential examples of the initial  
433 processes that drive plant species divergence at range limits via the budding model of  
434 speciation. Genetic and adaptive trait variation in the 11 species we have studied would  
435 provide fascinating information for our knowledge of potentially ongoing speciation  
436 processes.

437         What is also interesting in this respect is that nearly all of the eleven studied species  
438 have their peripheral populations located in highly localized zones (see Fig. 1) that could  
439 have served as potential refugia for Mediterranean taxa during the Last Glacial Maximum  
440 (near Narbonne to the east, north of Marseille and in the southern tip of the Maritime Alps).  
441 These zones host many endemic species (G. Papuga, unpublished data), and other studies  
442 illustrate a genetic footprint (population differentiation) in relation to range contraction and  
443 persistence in micro-refugia in Mediterranean France (Affre *et al.*, 1997; Diadema *et al.*,  
444 2005; Minuto *et al.*, 2006). Therefore, the configuration and geo-climatic history of the  
445 western Mediterranean have indeed been such that peripheral isolates of the species we  
446 have studied could have also been historical glacial refugia. Our cross taxa study set the  
447 scene to test ongoing speciation events.

#### 448 Conservation value of peripheral populations

449 The conservation value of peripheral populations remains controversial. Using resources to  
450 protect widespread species in regions where they are rare, what Hunter & Hutchinson  
451 (1994) named “parochialism” conservation, may be inefficient (due to their rarity, small  
452 population size and marginality) unless peripheral populations show genetic distinctiveness

453 or have some form of cultural value (Lesica & Allendorf, 1995; Leppig & White, 2006).  
454 Indeed, peripheral populations may contain unique gene combinations that result from  
455 either isolation (Lesica & Allendorf, 1995; Petit *et al.*, 1998) or hybridization with closely  
456 related species (Thompson *et al.*, 2010; 2017). However, the lack of precise knowledge  
457 regarding the ecology of plant species at their range periphery compared to elsewhere in  
458 their distribution has limited a more fuller understanding of the evolutionary significance of  
459 peripheral populations (Woodward, 1987; Crawford, 2010). The ecological originality of  
460 peripheral populations and their geographical isolation from the main area of their  
461 distribution we document here provide new arguments for the conservation significance of  
462 the listed species we studied, particularly in view of the need to conserve front-edge  
463 populations that may contribute to species' adaptation to ongoing climate change  
464 (Parmesan *et al.*, 2005).

465 However, the peripheral populations we have studied occur close to the Mediterranean  
466 coast and as a consequence of the rapidly growing human population (both permanent and  
467 seasonal) their habitats are now highly vulnerable and greatly impacted by land-use changes.  
468 Many populations of species in these habitats currently undergo translocation trials as their  
469 populations disappear from the landscape. For these species, our results show that the  
470 precise ecological conditions in microsites where plants occur are likely to be a critical  
471 determinant in the success of translocation trials to reinforce and reintroduce new  
472 populations. Broad-scale characterisation of their habitat is of limited use in guiding such  
473 projects. Hence, as Jusaitis (2005) pleaded, careful attention should be paid to the "exact  
474 placement" of such trials in natural areas.

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481 information on plant populations.

## 482 **List of brief titles of items in the supplementary material**

483 Appendix S1. Sampling sites

484 Appendix S2.

485 Appendix S3.

486 Appendix S4.

487 Appendix S5.

488 Appendix S6.

489 Appendix S7.

490 Appendix S8.

## 491 **Data accessibility assessment**

492 Data are freely accessible on request to the corresponding author.

## 493 **Biosketch (30 – 100 words)**

494 G.P. is a plant ecologist, working specifically on the ecology, evolution and conservation of  
495 Mediterranean species. He defended his PhD under the supervision of John Thompson and  
496 Emmanuele Farris. He is interested in plant ecology from local scale of plant-environment  
497 interactions, to more large-scale patterns of species distributions and range limits.

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698 **Tables**

699 **Table 1: List of studied species, their biological features and distances among sampled populations.** The nomenclature follows the most recent taxonomic  
 700 referential of the Mediterranean Botanical Conservancy (<http://silene.eu>)

N°	Species	Family	Flowering month	Biological type	Quadrat size (m <sup>2</sup> )	Mean and maximum distance among peripheral populations (km)		Mean and maximum distance among central populations (km)	
1	<i>Atractylis cancellata</i> L.	Asteraceae	Late spring	Therophyte	1	97	193	199	400
2	<i>Chiliadenus glutinosus</i> (Lam.) Brullo	Asteraceae	Autumn	Hemicryptophyte	4	32	60	87	172
3	<i>Convolvulus lanuginosus</i> Desr.	Convolvulaceae	Late spring	Hemicryptophyte	4	125	212	169	360
4	<i>Dorycnopsis gerardi</i> (L.) Boiss.	Fabaceae	Late spring	Hemicryptophyte	4	192	323	70	105
5	<i>Hyoseris scabra</i> L.	Asteraceae	Mid-spring	Therophyte	1	71	175	77	182
6	<i>Merendera filifolia</i> Cambess.	Colchicaceae	Autumn	Geophyte	1	1	3	105	185
7	<i>Narcissus dubius</i> Gouan	Amaryllidaceae	Early Spring	Geophyte	4	83	155	145	271
8	<i>Ophrys bombyliflora</i> Link	Orchidaceae	Mid Spring	Geophyte	1	12	25	142	266
9	<i>Polygala rupestris</i> Pourr.	Polygalaceae	Mid spring	Chamephyte	1	78	177	340	603
10	<i>Stipa capensis</i> Thunb.	Poaceae	Late spring	Therophyte	4	123	204	148	292
11	<i>Viola arborescens</i> L.	Violaceae	Autumn	Chamephyte	1	88	217	319	617

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704 **Table 2: The different broad habitat types occupied by the 11 study species in five central (C) and five peripheral (P) populations** in terms of the number  
 705 of populations sampled in each habitat (EUNIS referential: <http://eunis.eea.europa.eu/habitats.jsp>). Species are: (1) *Atractylis cancellata*, (2) *Chiliadenus*  
 706 *glutinosus*, (3) *Convolvulus lanuginosus*, (4) *Dorycnopsis gerardi*, (5) *Hyoseris scabra*, (6) *Merendera filifolia* (7) *Narcissus dubius* (8) *Ophrys bombyliflora*, (9)  
 707 *Polygala rupestris*, (10) *Stipa capensis*, (11) *Viola arborescens*.

EUNIS	Habitat	Species																					
		1		2		3		4		5		6		7		8		9		10		11	
		C	P	C	P	C	P	C	P	C	P	C	P	C	P	C	P	C	P	C	P		
A2.5	Coastal saltmarshes and saline reedbeds																2						
E1.2A	<i>Brachypodium phoenicoides</i> swards																3						
E1.31	West Mediterranean xeric grassland	5	5			5	5			4	4	5	5	5	5	3			5	4	4	2	3
E1.42	<i>Lygeum spartum</i> steppes																						1
E1.61	Mediterranean subnitrophilous grass communities									1							1			1	1		
E5.12	Weed communities of recently abandoned urban and suburban constructions										1												
E5.15	Land reclamation forb fields							5	5														
E6.12	Mediterranean <i>Lygeum spartum</i> salt steppes																						
F6.11	Western <i>Quercus coccifera</i> garrigues																		1				
G3.73	<i>Pinus pinea</i> forest																					1	
G3.74	<i>Pinus halepensis</i> forests																1					1	
H3.21	Tyrrheno-Adriatic eumediterranean calcicolous chasmophyte communities																		4			1	1

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710 **Table 3: The altitudinal range** (in meters) **of the 11 studied species** based on population locations in several databases for each species (see methods). The  
711 “minimum” and “maximum” columns correspond to the lowest and highest altitude values respectively, “lower limit” and “higher limit” are two limits that  
712 exclude 5% of data points for altitudinal distribution of each species at low and high altitude respectively. Hence, 90% of the data points occur between  
713 these limits.

	Central Populations					Peripheral populations				
	Minimum	Lower limit	Median	Upper limit	Maximum	Minimum	Lower limit	Median	Upper limit	Maximum
<i>Atractylis cancellata</i>	0	40	283	822	2414	12	14	361	558	585
<i>Chiliadenus glutinosus</i>	0	201	822	1315	1879	0	76	313	656	861
<i>Convolvulus lanuginosus</i>	0	87	462	1021	2822	0	1	121	344	493
<i>Dorycnopsis gerardi</i>	0	40	411	988	1356	0	4	111	304	495
<i>Hyoseris scabra</i>	0	10	180	814	1019	0	0	21	301	409
<i>Merendera filifolia</i>	0	3	310	1130	1663	0	2	21	30	32
<i>Narcissus dubius</i>	0	69	397	902	1378	0	19	171	519	788
<i>Ophrys bombyliflora</i>	0	7	321	815	1109	0	2	47	189	291
<i>Polygala rupestris</i>	0	84	585	1127	1959	0	0	54	223	559
<i>Stipa capensis</i>	0	15	382	831	1895	0	2	48	392	553
<i>Viola arborescens</i>	0	0	150	719	923	0	0	45	219	326

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716 **Table 4. Comparative analysis of ecological difference between central and peripheral populations in 11 Mediterranean plant species.** Welch two sample  
717 t-tests are used for pairwise comparisons (t-values) and analysis of deviance based on  $\chi^2$  analyses for cross taxa analyses. The number of species (NSP) and  
718 variables that show a significant difference are the row and column sums respectively. Species are: (1) *Atractylis cancellata*, (2) *Chiliadenus glutinosus*, (3)  
719 *Convolvulus lanuginosus*, (4) *Dorycnopsis gerardi*, (5) *Hyoseris scabra*, (6) *Merendera filifolia* (7) *Narcissus dubius* (8) *Ophrys bombyliflora*, (9) *Polygala*  
720 *rupestris*, (10) *Stipa capensis*, (11) *Viola arborescens*.

Niche characteristics	Species												NSP	Analysis of deviance	
	1	2	3	4	5	6	7	8	9	10	11	$\chi^2$			
S1. Water retention capacity	-5,3**	-4,41**	2,92**	-0,73	-0,35	-1,64	-2,33*	1,89	1,59	-0,62	2,19*	5	0,19		
S2. Conductivity	-0,37	0,93	3,89**	2,23*	2,28*	-3,41**	-4,2**	3,13**	2,47*	1,67	2,23*	8	6,07*		
S3. pH	4,46**	-0,27	-0,24	-3,18**	-0,36	-7,41**	2,73**	2,09*	-1,89	3,66**	-5,58**	7	4,50*		
A4. Rock	-3,85**	-3,94**	2,75*	1,31	4,40**	-0,82	1,52	0,94	2,84**	-2,03	3,05**	6	4,33*		
A5. Stone	-1,66	0,92	-4,02**	-0,68	0,66	-2,66*	-0,49	-2,56*	-4,63**	-1,21	-2,16*	5	11,91**		
A7. Gravel	1,73	3,43**	-4,68**	-2,55*	0,7	2,39*	-3,4**	-2,27*	-1,35	-0,92	0,06	6	0,22		
A8. Bare soil	3,33**	-0,21	1,93	0,75	-0,2	-0,8	-0,95	1,97	2,32*	0,48	0,26	2	2,22		
A9. Litter	3,14**	2,51*	2,36*	1,68	-2,29*	2,29*	-0,26	-0,01	0,68	-4,62**	-2,27*	7	0,01		
A10. Slope	-1,02	-4,5**	2,89**	2,06	4,14**	4,52**	-3,3**	1,99	6,47**	-0,82	2,28*	7	1,94		
B11. Total biotic cover	-2,05	2,41*	-0,03	0,42	-5,59**	-1,26	0,9	3,34**	-0,23	3,70**	-0,07	4	0,03		
B12. Therophyte cover	-0,38	0,96	-2,71*	1,52	-5,62**	-1,32	-4,01**	1,13	0,56	3,02**	1,2	4	0,65		
B13. Hemicryptophyte cover	-6,05**	1,66	1,23	-1,04	0,4	-0,8	1,7	0,87	-1,18	-0,35	0,43	1	0,00		
B14. Geophyte cover	2,54*	1	-0,06	1,95	1,91	0,49	0,52	0,79	-2,03	1,77	-2,98**	2	0,51		
B15. Woody vegetation cover	1,32	1,99	-1,04	0,34	-0,73	-2,34*	0,55	-0,63	0,86	-1,69	0,08	1	0,11		
B19. Cryptogams cover	NA	-1	1,6	0,64	-1,65	0,8	2,72*	0,04	1,03	0,93	-1,16	1	0,69		
B16. Total diversity	-3,26**	2,62*	0,11	-2,97**	-3,64**	-0,28	-2,69**	2,61*	0,59	-4,00**	1,88	7	3,98*		
B17. Diversity of therophytes	-2,29*	NA	-2,42*	-1,32	-6,63**	-2,09*	-4,01**	0,31	-0,21	-4,57**	0,8	6	22,30**		
B18. Diversity of hemicryptophytes	-2,54*	0,11	3,85**	-4,14**	0,9	2,08*	-1,65	1,77	1,1	-1,54	2,48*	5	0,01		
B19. Diversity of geophytes	1,77	NA	-1,9	1	3,28*	0,02	0,69	4,58**	-0,05	1,83	NA	2	6,41*		

B20. Diversity of woody plants	0,4	1,75	1,16	0,32	0,23	-0,77	0,02	-1,47	-0,7	-2,20*	0,67	1	0,01
Number of variables	10	7	10	5	9	9	9	7	5	7	9		

721 \* :  $0.05 > p >$  corrected significance level, \*\* :  $p <$  Corrected significance level.

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725 **Table 5. Comparative analysis of niche variability among central and among peripheral populations in eleven Mediterranean plant species.** Ansari-Bradley  
726 tests are used for pairwise comparisons, and single tail Wilcoxon test are used to assess for a greater niche volume for central population. The numbers of  
727 species (NSP) and variables that show a significant difference are given in row and column sums respectively. Species are: (1) *Atractylis cancellata*, (2)  
728 *Chiliadenus glutinosus*, (3) *Convolvulus lanuginosus*, (4) *Dorycnopsis gerardi*, (5) *Hyoseris scabra*, (6) *Merendera filifolia* (7) *Narcissus dubius* (8) *Ophrys*  
729 *bombyliflora*, (9) *Polygala rupestris*, (10) *Stipa capensis*, (11) *Viola arborescens*.

Niche characteristics	Species											NSP	Wilcoxon test V
	1	2	3	4	5	6	7	8	9	10	11		
S1. Water retention capacity	107	133	113	130	126	85*	111	92*	93*	120	149*	4	55
S2. Conductivity	112	104,5	133	102,5	121	87*	112	103	119	138	144*	2	43
S3. pH	101	126,5	98	94*	140,5	115	119	107	109,5	130	120	1	50
A4. Rock	111,5	125	103	155	117	98,5*	129,5	185*	118	132,5	101,5	2	21
A5. Stone	93	132,5	124	124,5	122	112,5	109	111,5	137	135	145*	1	56*
A7. Gravel	84*	124	120	135,5	147*	114	125,5	110,5	109,5	127,5	120	2	52
A8. Bare soil	121	143,5*	108,5	117	149*	142	130,5	109	124	107	104	2	17
A9. Liter	108	111	132,5	117	128	135	124	104	106	105	92*	1	32
A10. Slope	120	128,5	130,5	142	107	117,5	142	99*	118	124,5	114	1	9*
B11. Total biotic cover	107	116,5	88*	112	125	122	138	127	92*	116	108	2	43
B12. Therophyte cover	131*	185*	138,5*	110	125	143,5	124,5	118	137,5	136	121	3	26
B13. Hemicryptophyte cover	114	120,5	116	121	117	130	98	111	92*	110	145*	2	38
B14. Geophyte cover	99	211*	106	145	111	109	111	126	148,5*	119	137*	3	24
B15. Woody vegetation cover	92	106	121,5	107,5	122,5	97*	96,5	118	110	117,5	97	1	57*
B19. Cryptogams cover	210*	131	133,5	165,5*	145	121	104,5	113,5	163	105	165*	3	31
B16. Total diversity	105	96*	131	96*	114	146*	110	108	134	120	122	3	37
B17. Diversity of therophytes	115	232,5*	158*	99	128	134,5	116,5	123	181,5*	135	186*	4	28
B18. Diversity of hemicryptophytes	107,5	96*	120	108	140	117	131	113	129	118,5	108	1	36
B19. Diversity of geophytes	156	232,5*	180*	211*	113	130	115	117,5	205*	174	232,5*	4	6

B20. Diversity of woody plants	116	118,5	132	104	122	133	108	134	125	181*	108	1	41
Number of variables	3	7	4	4	2	5	0	3	6	1	9		

730 Note. For statistical tests, \* :  $0.05 > p >$  corrected significance level,.

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## 737 **Figures**

738 Figure 1. Distribution maps of the 11 studied species in the western Mediterranean basin. Black dots  
739 are locations sampled for the field survey; grey areas represent the distribution of each species  
740 adapted from Bolos & Vigo (2000).

741 Figure 2. Mean (a) and range (b) of altitude values (in meters) for central and peripheral populations  
742 of 11 Mediterranean plant species. The bisector represents equal mean values for central and  
743 peripheral populations. Species code numbers are listed in Table 1.

744 Figure 3. Soil characteristics, abiotic and biotic cover variables that show overall significant  
745 differences (Table 4) among central and peripheral populations of 11 Mediterranean plant species.  
746 The bisector represents equal mean values for central and peripheral populations. Traits are (a) soil  
747 conductivity, (b) pH, (c) rock cover, (d) stone cover, (e) total biotic cover, (f) species diversity, (g)  
748 therophyte diversity, (h) geophyte diversity. Species number codes are listed in table 1.

749 Figure 4. Comparison of levels of variation in niche volume among central and among peripheral  
750 populations of 11 Mediterranean plant species: (a) overall niche volume including biotic, abiotic and  
751 soil variables, (b) soil characteristics, (c) biotic characteristics, (d) abiotic traits. The bisector  
752 represents equal values for central and peripheral populations. Species number codes are listed in  
753 Table 1.

754

## 755 **Supporting information**

756 Appendix S1: sampling sites

757 Appendix S2.

758 Appendix S3.

759 Appendix S4.

760 Appendix S5.

761 Appendix S6.

762 Appendix S7.

763 Appendix S8.