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Original
Ecological niche differentiation in peripheral populations: a comparative analysis of eleven Mediterranean plant species / Papuga, G., Gauthier, P., Pons, V., Farris, E., Thompson, J.D.. - In: ECOGRAPHY. - ISSN 0906-7590. - 41:(2018), pp. 1650-1664. [10.1111/ecog.03331]

Availability:
This version is available at: 11388/212431 since: 2022-05-26T17:02:07Z

Publisher:

Published
DOI:10.1111/ecog.03331

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note finali coverpage

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12 October 2026

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

Papuga G.[1,2,3], Gauthier P.[2], Pons V.[2], Farris E.[1], & Thompson J.D.[2]

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

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

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

Keywords: ecological niche; centre-periphery hypothesis; Mediterranean; range limits; budding speciation; parochialism; conservation

Short running title: Ecological niche shift in Mediterranean plants

Author for correspondence: Guillaume Papuga

Email: guillaume.papuga@gmail.com

Number of words in the abstract: 244

Number of words in the main body of the paper: 5104

Number of references: 77

Abstract

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

Location: Western Mediterranean basin

Time Period: 2013-2014

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

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

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

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

Introduction

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

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

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

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

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

Material and methods

Species and population selection

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

We then restricted the list to species that exhibit a clear central-peripheral type of distribution, with a central part of their range in the Iberian or Italian peninsula and/or North Africa and northern peripheral populations in the Mediterranean climate region of France. 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 Ecologia (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 < 1km^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

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

Field and database examination of the macro niche

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

Field investigation of fine-scaled niche characteristics

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

The ecological characteristics of each quadrat were determined with point contact data for 100 contact points (10*10cm grid for $1m^2$ quadrats; 20*20cm grid for $4m^2$ 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 pf 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 (± 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.*,

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

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

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

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

Results

Macro niche

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

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

Fine-scaled niche characteristics

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

The comparison of central and peripheral populations for each species showed significant differences for between five and ten of the 20 of the analyzed ecological variables per species (Tab. 4). On average, eight variables per species showed significant variation between central and peripheral populations. Seven ecological variables (mostly biotic) showed very little variation, with no more than two species showing significant differences per variable. On average, soil characteristics and abiotic cover variables (other than bare soil) showed more significant differences (five to eight species) than biotic variables. All species showed at least one significant difference for soil characteristics and abiotic cover variables (Tab. 4). The total diversity of associated species and therophyte diversity showed significant differences for seven and six species respectively, as did total biotic cover and therophyte cover, but only for four species. Despite the large number (5-10 traits) of observed significant differences for each species (Tab. 4), only *Convolvulus lanuginosus, Hyoseris 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

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

Ecological originality of peripheral populations

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

In direct contrast, significant variation in the micro-ecological niche between central and peripheral populations was found for between five and ten of the 20 variables (on average eight ecological variables per species) and all the studied ecological variables exhibit significant differences for at least one species (Appendix S5 for complementary analysis). Soil characteristics and abiotic cover variables showed the highest number of significant differences between central and peripheral populations, while biotic cover variables were less variable. Despite overall broad habitat similarity, the study species thus show marked ecological originality in terms of their precise ecological niche in peripheral populations. This 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,

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

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

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

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

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

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

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

Ecological differentiation and species divergence

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

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

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

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

Conservation value of peripheral populations

The conservation value of peripheral populations remains controversial. Using resources to protect widespread species in regions where they are rare, what Hunter & Hutchinson (1994) named “parochialism” conservation, may be inefficient (due to their rarity, small 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.

475 ## Acknowledgements

We thank the technical staff at the CEFE whose facilities are part of the CEMEB (*Plateforme d'Analyse Chimique en Ecologie* for soil analyses and the *Terrain d'Experimentation)* for technical support. We thank Simone Dessena, Alfredo Maccioni and Chiara Chelo for their help in the field, and Frederic Andrieu (Conservatoire Botanique Méditerranéen de Porquerolles), Juan Arroyo, Benoit Bock, Emilio Laguna, Gonzalo Mateo Sanz, for providing information on plant populations.

List of brief titles of items in the supplementary material

Appendix S1. Sampling sites

Appendix S2.

Appendix S3.

Appendix S4.

Appendix S5.

Appendix S6.

Appendix S7.

Appendix S8.

Data accessibility assessment

Data are freely accessible on request to the corresponding author.

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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697

Tables

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

N°	Species	Family	Flowering month	Biological type	Quadrat size (m²)	Mean and maximum distance among peripheral populations (km)		Mean and maximum distance among central populations (km)	
1	*Atractylis cancellata* L.	Asteraceae	Late spring	Therophyte	1	97	193	199	400
2	*Chiliadenus glutinosus* (Lam.) Brullo	Asteraceae	Autumn	Hemicryptophyte	4	32	60	87	172
3	*Convolvulus lanuginosus* Desr.	Convolvulaceae	Late spring	Hemicryptophyte	4	125	212	169	360
4	*Dorycnopsis gerardi* (L.) Boiss.	Fabaceae	Late spring	Hemicryptophyte	4	192	323	70	105
5	*Hyoseris scabra* L.	Asteraceae	Mid-spring	Therophyte	1	71	175	77	182
6	*Merendera filifolia* Cambess.	Colchicaceae	Autumn	Geophyte	1	1	3	105	185
7	*Narcissus dubius* Gouan	Amaryllidaceae	Early Spring	Geophyte	4	83	155	145	271
8	*Ophrys bombyliflora* Link	Orchidaceae	Mid Spring	Geophyte	1	12	25	142	266
9	*Polygala rupestris* Pourr.	Polygalaceae	Mid spring	Chamephyte	1	78	177	340	603
10	*Stipa capensis* Thunb.	Poaceae	Late spring	Therophyte	4	123	204	148	292
11	*Viola arborescens* L.	Violaceae	Autumn	Chamephyte	1	88	217	319	617

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 of populations sampled in each habitat (EUNIS referential: http://eunis.eea.europa.eu/habitats.jsp). Species are: (1) *Atractylis cancellata, (2) Chiliadenus glutinosus, (3) Convolvulus lanuginosus, (4) Dorycnopsis gerardi, (5) Hyoseris scabra, (6) Merendera filifolia (7) Narcissus dubius (8) Ophrys bombyliflora, (9) Polygala rupestris, (10) Stipa capensis, (11) Viola arborescens.*

		Species																					
EUNIS	Habitat	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	C	P
A2.5	Coastal saltmarshes and saline reedbeds															2							
E1.2A	*Brachypodium phoenicoides* 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	*Lygeum spartum* 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 *Lygeum spartum* salt steppes																						
F6.11	Western *Quercus coccifera* garrigues																	1					
G3.73	*Pinus pinea* forest																					1	
G3.74	*Pinus halepensis* forests																1						1
H3.21	Tyrrheno-Adriatic eumediterranean calcicolous chasmophyte communities			5	5													4				1	1

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

714

715

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

Niche characteristics	Species												Analysis of deviance
	1	2	3	4	5	6	7	8	9	10	11	NSP	χ^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. Liter	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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Table 5. Comparative analysis of niche variability among central and among peripheral populations in eleven Mediterranean plant species. Ansari-Bradley 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 species (NSP) and variables that show a significant difference are given in row and column sums respectively. Species are: (1) *Atractylis cancellata, (2) Chiliadenus glutinosus, (3) Convolvulus lanuginosus, (4) Dorycnopsis gerardi, (5) Hyoseris scabra, (6) Merendera filifolia (7) Narcissus dubius (8) Ophrys bombyliflora, (9) Polygala rupestris, (10) Stipa capensis, (11) Viola arborescens.*

Niche characteristics	Species											NSP	*Wilcoxon test*
	1	2	3	4	5	6	7	8	9	10	11		V
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		

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

Figures

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

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

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

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

Supporting information

Appendix S1: sampling sites

Appendix S2.

Appendix S3.

759 Appendix S4.

760 Appendix S5.

761 Appendix S6.

762 Appendix S7.

763 Appendix S8.