

# Ecological Research

## Plant functional traits and groups in a Californian serpentine Chaparral

--Manuscript Draft--

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<b>Abstract:</b>	<p>We studied a type of Californian ultramafic chaparral to determine functional groups which can help reduce the complexity of ecosystem management. The study was realized in McLaughlin Reserve, State of California, USA. We analysed the species of a serpentine plant association previously phytosociologically described in the area: <i>Ceanotho albiflori-Quercetum duratae</i> for their functional traits and functional groups. Traits per species were measured building a trait database. We used Principal Component Analysis to identify the combination of functional traits with major weight and a neighbor-joining clustering to define functional groups for this vegetation association. Our results indicated that the studied association is dominated by phanerophytes, with low degree of spinescence. Leaves were mainly malacophyllous with high degree of tomentosity, reduced size and a partial shedding of leaves was observed during summer. We considered six functional groups as the optimum number of clusters in a total of 18 species. The two first functional groups were composed of chamaephytes with brachyblasts and dolichoblasts with differences in the degree of tomentosity. The rest of the functional groups were composed of phanerophytes where the differences between them were based on traits in relation to the branches, leaf size and the horizontal development of the root system. The functional groups obtained show that this serpentine chaparral is composed of species with a wide range of functional traits. The study of other Mediterranean serpentine ecosystems in California and elsewhere could contribute to create new perspectives of functional ecology and help in the management of these valuable ecosystems.</p>
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## Responses to the reviewer comments

All the reviewer comments have been carefully considered and accepted in the new MS. They were mainly grammatical changes and other questions related to sentences difficult to understand in their meaning.

The grammatical changes have been highlighted in the new version of the MS by the track changes.

The sentences difficult to understand have been highlighted in the text by the track changes and are commented below:

### 1.- “the spread of the root system”:

This expression has been replaced (in the main text and in appendix 1) for the suggested expression: horizontal development of the root system.

### 2. “Keywords”:

“Californian serpentine chaparral” has been replaced by “ultramafic Chaparral”.

### 3. “Serpentinite or Peridotite? From the mineralogical it is Serpentinite. Please use serpentinite here. Not needed further in the sentence”.

We agree with this suggestion, serpentinite is the correct assumption.

### 4. “If this value was high to a specific component”,

We have reworded the sentence, we agree with the reviewer that the previous was not precise. The new sentence proposed is: “If this value was high for one of the specific component”

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1           **Plant functional traits and groups in a Californian serpentine Chaparral**

2

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14

15 **Abstract**

16 We studied a type of Californian ultramafic chaparral to determine functional  
17 groups which can help reduce the complexity of ecosystem management. The  
18 study was realized in McLaughlin Reserve, State of California, USA. We  
19 analysed the species of a serpentine plant association previously  
20 phytosociologically described in the area: *Ceanotho albiflori-Quercetum duratae*  
21 for their functional traits and functional groups. Traits per species were measured  
22 building a trait database. We used Principal Component Analysis to identify the  
23 combination of functional traits with major weight and a neighbor-joining  
24 clustering to define functional groups for this vegetation association. Our results  
25 indicated that the studied association is dominated by phanerophytes, with low

26 degree of spinescence. Leaves were mainly malacophyllous with high degree of  
27 tomentosity, reduced size and a partial shedding of leaves was observed during  
28 summer. We considered six functional groups as the optimum number of clusters  
29 in a total of 18 species. The two first functional groups were composed of  
30 chamaephytes with brachyblasts and dolichoblasts with differences in the degree  
31 of tomentosity. The rest of the functional groups were composed of phanerophytes  
32 where the differences between them were based on traits in relation to the  
33 branches, leaf size and the horizontal development of the root system. The  
34 functional groups obtained show that this serpentine chaparral is composed of  
35 species with a wide range of functional traits. The study of other Mediterranean  
36 serpentine ecosystems in California and elsewhere could contribute to create new  
37 perspectives of functional ecology and help in the management of these valuable  
38 ecosystems.

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39 **Keywords:** ultramafic Chaparral; functional traits; functional groups; adaptations;  
40 Mediterranean climate.

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41

#### 42 **Abbreviations:**

43 PCA: Principal component analysis; FG: functional groups; NDVI: Normalized  
44 Difference Vegetation Index; CD: Crown diameter, DC: Canopy density in %;  
45 LSD and LSB: Leaf size in cm<sup>2</sup> –larger and smaller leaves; H: Plant height; M:  
46 Morphology of aerial part; T: Leaf tomentosity; PS: Leaf area/Assimilating stem  
47 area-ratio; SR: Spread (horizontal development) of root system; F: Vegetative  
48 regeneration after fire; BT: Branch type; DR: Depth of root system; RB: Location  
49 of renewal buds; S: Spinescence; SE: strict endemic; BE: broad endemic; BE/SI:  
50 broad endemic/strong indicator; SI: strong indicator; WI: weak indicator; WI/IN:  
51 weak indicator/indifferent.

52 **Introduction**

53 Throughout the world, serpentine or ultramafic soils support distinctive vegetation  
54 and unique endemic species (Brooks 1987; Proctor and Woodell 1975; Roberts  
55 and Proctor 1992; Baker et al. 1992; Kruckeberg 2002). One of the world's richest  
56 serpentine floras is found in the Californian Floristic Province (the Mediterranean-  
57 climate region encompassing most of California, USA, and small territories in  
58 adjacent Oregon and Mexico), which contains at least 246 serpentine endemic  
59 plant taxa (Safford et al. 2005). These species are found in a variety of vegetation  
60 types including forests, woodlands, sclerophyllous shrublands ("chaparral") and  
61 grasslands (Barbour and Major 1977; Kruckeberg 1984, 2006; Harrison et al.  
62 2006; Alexander et al. 2007; Grace et al. 2007).

63 We focus on California's serpentine chaparral, a complex of Mediterranean  
64 shrub-dominated vegetation types (Anacker et al. 2011) that covers 8.5% of  
65 California (Barbour and Major 1977; Keeley and Soderstrom 1986) and consisting  
66 of five vegetation types, defined as 'serpentine or ultramafic chaparrals'. They are  
67 considered as xero-edaphic climax vegetation in the phytosociological alliance  
68 *Quercion duratae* (*Heteromelo arbutifoliae-Quercetea agrifoliae* class). The  
69 floristic structure of this potential vegetation is composed by the leather oak  
70 (*Quercus durata*), the dominant character species, and by companion evergreen  
71 sclerophyllous shrubs, of which the next most frequent species are from the  
72 genera *Arctostaphylos* and *Ceanothus* (Sánchez-Mata and Rodríguez-Rojo 2016).  
73 We focus on one of the types, the interior northwest California serpentine  
74 chaparral. Serpentine chaparral has exclusive adaptations to ultramafic soils which  
75 have been described **generally** (Brady et al. 2005; Kazakou et al. 2008).

76 Ecosystem ecologists have long recognized the functional traits of organisms  
77 as key drivers of ecosystem properties (Jones and Lawton 1995). Studies of  
78 functional types in relation to climate are common; in the Mediterranean area,

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79 they were designed to study how the plants manage to survive in the summer to  
80 the typical Mediterranean drought: these are the arid-active species, which still  
81 have a photosynthetic green part in the summer and therefore have no choice but  
82 to show adaptations to survive which correspond with certain functional types  
83 (Evenari et al. 1975; Orshan 1986). However, specific studies on the functional  
84 traits of plants in relation to serpentine soils are rare. Some of the general traits  
85 identified for serpentine endemics are (Kruckeberg 1984; Brooks 1987; Tibbets  
86 and Smith 1992; Brady et al. 2005): (1) reduced leaf size, for instance lower  
87 specific leaf area -SLA- in herbaceous species (Adamidis et al. 2014), and  
88 sclerophylly and reduced SLA in serpentine Californian chaparral (Ackerly et al.  
89 2002; Anacker et al. 2011); (2) Leaf succulence (Harrison and Rajakaruna 2011);  
90 (3) Smaller stature (Hanes 1981; Kruckeberg 1984; Brooks 1987; Tibbets and  
91 Smith 1992; Brady et al. 2005); (4) Down-regulation of lateral root growth due to  
92 the high content in Mg; (5) Slow growth rates (Kruckeberg 1984; Tibbets and  
93 Smith 1992; Brady et al. 2005) and big root (high root biomass or strongly  
94 developed root systems; Harrison and Rajakaruna 2011). Finally, with respect to  
95 adaptations to fire, serpentine soils can support populations of regionally or  
96 locally rare plants that appear to be escaping competition and/or frequent fire  
97 (Safford and Harrison 2004).

98 One of the goals of knowing of the adaptive characters of the components  
99 (species) of the ecosystems (Mooney 1974; Le Roux et al. 1984; Pierce 1984) is  
100 to detect functional groups of species (FG) (Herrera 1984). Functional groups are  
101 sets of plants exhibiting similar responses to environmental conditions and having  
102 similar effects on the dominant ecosystem processes (Walker 1992; Noble and  
103 Gitay 1996; Díaz and Cabido 1997; Boulangeat et al. 2012). With the help of  
104 functional groups we are able to summarize the enormous complexity of  
105 individual species and populations into a relatively small number of general

106 recurrent groups (Walker 1992; Grime et al. 1997). This approach is highly  
107 relevant to the assessment of ecosystem function (Gitay and Noble 1997) by  
108 allowing the generalization of ecosystems to a limited number of functional  
109 groups instead of dealing with a large number of species (Grime et al. 1996; Díaz  
110 Barradas et al. 1999; Petchey 2004).

111 Reduced functional group diversity often occurs in high resource  
112 environments. Contrastingly dry and infertile serpentine soils are dominated by a  
113 mixture of functional groups (Hobbie et al. 2012). In California, studies of  
114 serpentine functional groups have been included different serpentine  
115 communities: grassland, chaparral and forest (Grace et al. 2007) and using  
116 ambient attributes like climate, soils and NDVI. On serpentine grassland,  
117 according to Fernández-Going et al. (2012), functional diversity was low and did  
118 not appear to play an important role in explaining the taxonomic diversity of plant  
119 communities. Serpentine communities may have higher levels of diversity  
120 (although sparser vegetation) in functional traits than communities on other types  
121 of soils, and this may confer resistance to several environmental stressors (Tilman  
122 and Downing 1994; McCann 2000).

123 Here, we identify the main functional characters (growth forms or  
124 ecomorphological types as functional traits) of 18 serpentine chaparral plant  
125 species and create a classification in groups of the plant functional types in this  
126 serpentine chaparral.

127

## 128 **Methods**

129

130 Study site

131 The study was realized in McLaughlin Reserve in the State of California, USA,  
132 throughout the summer months of 2014. This Reserve, with an area of 27.76 km<sup>2</sup>,  
133 is one of few sites in California that protects unusual serpentine habitats. Situated  
134 in Napa, Yolo and Lake Counties, at the boundary of the Putah and Cache Creek  
135 watersheds (Fig. 1).

136

137 **Fig. 1** Location of the study plot in the McLaughlin Reserve (State of California,  
138 USA.). The green square is the plot, the brown circle is the field station and blue  
139 line is the Reserve boundary. Modified from Farm service agency data

140

141 McLaughlin Reserve has a geological composition predominantly  
142 consisting of serpentine which permitted us to choose a serpentine vegetation  
143 plot (20\*20 m<sup>2</sup>), in the Knoxville area located at an altitude of 630 m. (UTM 10S  
144 550179E/ 4302959 N). The serpentine mineral group is lizardite, chrysotile and  
145 antigorite (University of California, Davis Natural Reserve System, 2003). The  
146 bioclimatic indexes (*It* and *Io*), based on Rivas Martinez (1996-2009), were  
147 calculated using data from the “Knoxville Creek California station” (38° 51' 43"/  
148 122° 25' 02"; 670 m) and resulting lower Mesomediterranean bioclimatic belt and  
149 ombrotype Subhumid- lower subhumid.

150

151 Sampling methods

152 Vegetation

153 The sample area was chosen taking into consideration the presence of the  
154 characteristic shrub species belonging to the selected chaparral type in a  
155 phytosociological sense (Boulangeat et al. 2012). In order to gather vegetation  
156 data, a selective plant inventory (Appendix S1) in the locality was made following

Commented [n6]:

157 Braun-Blanquet instructions (1979), including environmental data, presence and  
158 cover of plant species. Among the five vegetation types defined as ‘ultramafic  
159 chaparrals’ in California by Sánchez-Mata and Rodríguez-Rojo (2016), our  
160 McLaughlin inventory showed that the study area contains the *Ceanotho albiflori-*  
161 *Quercetum duratae* (chaparral association) Sánchez-Mata, Barbour and  
162 Rodríguez-Rojo in Rivas-Martínez 1997 (*Quercion duratae* or *Quercus durata*  
163 Alliance by Sawyer et al. 2009, *Adenostomo fasciculatae-Rhamnnetalia croceae*,  
164 *Heteromelo arbutifoliae-Quercetea agrifoliae*). The area of the selected plot  
165 (20\*20m<sup>2</sup>) exceeds the minimum area necessary to include the theoretical whole  
166 diversity of species for shrubland vegetation (Braun-Blanquet 1979; Sawyer et al.  
167 2009; Sánchez-Mata and Rodríguez-Rojo 2016), and for the ultramafic  
168 associations. Species were selected from the 20x20 meter area.

169

#### 170 Studied species

171 Eighteen species found in the plot and belonging to the plant association were  
172 selected for analysis (Table 1, Fig. 2) (phytosociological inventory, Appendix S1),  
173 using robust and well grown individuals, located in well-lit environments, and  
174 partially unshaded (Cornelissen et al. 2003). Following recommendations made  
175 by Orshan (1986), we only took persistent, arid-active perennial species into  
176 account (Evenari et al. 1975), which are those bearing aerial active shoots  
177 throughout the year and which show therefore adaptations to the Mediterranean  
178 dry season. In this case, those include shrubs (phanerophytes), smaller shrubs and  
179 a part of the perennial herb species (chamaephytes) of the plot. *Pinus sabiniana*,  
180 which was present in the studied community as scattered trees (inventory,  
181 Appendix S1), belonging to a different Alliance to the chaparral (Sawyer et al.  
182 2009), was not included in our study.

183 Ten individuals from each species were measured in the field and voucher  
184 specimens from the UC Davis Herbarium were used for laboratory measures.  
185 Botanical nomenclature followed mainly Barbour and Major (1977), Baldwin et  
186 al. 2012, but further we used USDA Plants Database, CALFLORA (2016) and the  
187 “list of the McLaughlin Reserve plants”, unpublished data (2014). Serpentine  
188 categories (affinity) following Safford et al. (2005) were indicated for each  
189 studied species (Table 1). Voucher specimens of the studied species were stored in  
190 the MGC Herbarium (University of Malaga, Spain).

191

192 **Table 1** List of studied species, families and serpentine categories (affinity)  
193 following nomenclature in Safford et al. (2005)

194

195 **Fig. 2** Photographs of the some species included in this study: **a)** *Arctostaphylos*  
196 *viscida*, **b)** *Ceanothus jepsonii*, **c)** *Quercus durata* var. *durata*, **d)** *Heteromeles*  
197 *arbutifolia*, **e)** *Rhamnus ilicifolia*, **f)** *Cercocarpus betuloides*, **g)** *Garrya*  
198 *congdonii*, **h)** *Eriodictyon californicum*, **i)** *Adenostoma fasciculatum*, **j)** *Frangula*  
199 *californica*, **k)** *Galium andrewsii*, **l)** *Castilleja foliolosa*. Photographs: N. Hidalgo-  
200 Triana

201

202 Studied functional traits (Ecomorphology)

203 For the ecomorphological characterization of each species, we studied 22  
204 ecomorphological measurable categorical traits using measures developed by  
205 Orshan (1982, 1986), Pérez Latorre and Cabezudo (2002), Cornelissen et al.  
206 (2003), and Pérez-Harguindeguy (2013) and using the ecological definitions  
207 provided by those authors. The measured traits are described in the Appendix S2.  
208 Some of the main characteristics include: photosynthetic organs (consistency,

209 tomentosity and size); below-ground organs (root system); longevity and  
210 seasonality; plant regeneration; multiplication and trophism along with fruit type  
211 (fleshy, dry); branch type (dolichoblast branches, defined as branches which grow  
212 following the annual cycle stretching more than 3 cm and brachyblast branches,  
213 defined as branches that show a limited growth each year, remaining as a very  
214 short branch state for months or years until they dry out or give rise to vegetative  
215 or reproductive dolichoblasts); and the morphology of the aboveground  
216 component. For standardization, the methods used for collection of functional  
217 traits mainly followed the worldwide handbook for standardized measurement of  
218 plant functional traits (Cornelissen et al. 2003; Pérez-Harguindeguy et al.  
219 2013). Appendix S2 includes descriptions of the methods used for each trait.

220 Once all of the traits per species were measured, we made the  
221 ecomorphological description of the plant association using percentage of  
222 presence in the studied species, intervals and the mean or the dominant attributes  
223 of the following characters suggested by Pérez Latorre and Cabezudo (2002):  
224 dominant renewal bud location, spinescence, stem consistency, plant height  
225 (stratification), organs periodically shed, seasonality of assimilating organs, type  
226 of branches (%), leaf consistency, leaf tomentosity (%), dominant interval of leaf  
227 size, leaf longevity, mean plant longevity and type of vegetative regeneration after  
228 fire.

229

230 Statistical analysis

231 In order to classify the species based on the main measurable characters, a data  
232 matrix was built to identify the major axes of variation in the functional traits of  
233 the studied species. The trait database was built for all species (18) and with the

234 quantitative and semi-quantitative traits (n = 14, Table 2; all of these variables are  
235 defined in the Appendix S2).

236 Prior to the analysis, the variables were typified (by subtracting the mean and  
237 dividing by the standard deviation) in order to avoid an unbalanced contribution  
238 of any of them.

239 We used principal component analysis (PCA), a multivariate ordination  
240 method, performed with the free software PAST (version 2.17, Hammer et al.,  
241 2001). PCA was calculated for each extract component with correlation  
242 (normalized var-covar) method using only the quantitative characters (RB, H, S,  
243 LSD, LSB, PS, S, DR, Table 2). If this value was high for one of the specific  
244 component, it would be interpreted as an indicator of the weight of the  
245 component. In addition, it serves to explain the total variance.

Commented [n7]:

246 A neighbor-joining clustering of the measurable variables (quantitative and  
247 semi-quantitative), based on Euclidean distances, was performed by using all the  
248 functional traits of the Table 2. Cluster analysis was realized with PAST in order  
249 to find functional groups (FG). The cluster cut level was determined manually so  
250 that the resulting groups were interpretable and in line with field observations of  
251 the traits.

Commented [n8]:

252 Strategies Richness index (*Sri*) is the relation between the number of  
253 functional groups or coenomorphs and the number of species into the plant  
254 community. It was calculated following Pérez Latorre et al. (2007).

255

256 **Table 2** Traits used in the PCA and in the cluster analysis

257

## 258 **Results**

259 Ecomorphological description of the community

260 This Shrub community is composed mainly of phanerophytes and shows a low  
261 degree of spinescence. The plants are mainly holoxyle, with a dominant height  
262 between 1-5 m., and representing a bi-stratified community. Species are mainly  
263 evergreen. In summer, a partial shedding of leaves is observed. 55% of plants  
264 have dolichoblasts leaves, 11% have brachyblasts leaves and 33% of plants have  
265 dolichoblasts and brachyblasts leaves. Leaves are mainly malacophyllous (61%)  
266 but some of them are sclerophyllous (17%) or semisclerophyllous (22%), with a  
267 tomentosity degree of 61%. Leaf size ranges between 0.25-12.25 cm<sup>2</sup> in  
268 dolichoblasts and in brachyblasts leaves are smaller (0.25-2.25 cm<sup>2</sup>) and lasting on  
269 6-14 months mainly. The longevity of plants is predominantly between 2-25  
270 years. Most of the plants have vegetative regeneration after fire by below ground  
271 organs (61%) and most of them can also regenerate by seeds (22%).

Commented [n9]:

272  
273 Results of the PCA: main functional traits of serpentine chaparral (characters)  
274 Eigenvalues of the different taxa for the two main components were represented  
275 in a biplot spatial diagram (Fig. 3). The PCA showed that two axis supported  
276 63.1% of the variance. The first axis is interpreted as reflecting a gradient of  
277 renewal buds, which is increasing towards bigger sizes on the right. On the  
278 positive direction of the second component where situated the species which had  
279 spinescence and, in several cases, photosynthetic stems.

Commented [n10]:

280  
281 **Fig. 3** Biplot spatial diagram with two axis: functional groups based on taxa. Solid  
282 black dots are the taxa. Characters are represented using abbreviations in Table 2  
283  
284 Component 1 corresponds with RB, H, DR, and LSD, while component 2 is  
285 related to S and PS

286 Results of the clustering analysis: Functional Groups (FG`s)

287 Our analysis identified six main functional groups (correlation coefficient 0.71;  
288 functional groups are shown in the Appendix S3: dendrogram and Table S3)  
289 coexisting in the studied community. The occurrence of six main functional  
290 groups (coenomorphs) in a total of 18 species corresponds to a *Sri* of 0.33.

291 At the first step of the cluster analysis, species were classified into two  
292 general groups: chamaephytes and phanerophytes. So, the position of renewal  
293 buds was very important to unravel functional diversity in this ecosystem. The  
294 following groups were based mainly on the presence of brachyblasts and  
295 dolichoblasts and on the rest of the traits as follows:

296 Functional Group (FG) 1: chamaephytes with brachyblasts and dolichoblasts  
297 but showing low degree of tomentosity.

298 FG 2: chamaephytes with brachyblasts and dolichoblasts but with high degree  
299 of tomentosity. The two species of *Galium* were included in FG 1 and FG 2 by the  
300 analyses according to the renewal position of buds, but they have only  
301 dolichoblasts branches and for this reason we could separate this taxon from this  
302 group in a subgroup.

303 FG 3, FG 4, FG 5 and FG 6 were phanerophytes, with big roots and big size  
304 (high values of plant height, canopy density and crown diameter) but traits as  
305 presence of dolichoblasts and brachyblasts, the leaf size and the extension of the  
306 root system splitted these groups.

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307 FG 3: phanerophytes, mainly with dolichoblasts only and all of them having  
308 tap roots except for *Rhamnus illicifolia*.

Commented [n12]:

309 FG 4 and FG 5: comprised of two amphiphytes but they were in different  
310 groups according to the presence/absence of spinescence and photosynthetic  
311 stems.

312 And finally, FG 6: included phanerophytes with horizontal and vertical roots,  
313 without vegetative regeneration after fire but with regeneration after fire by seeds  
314 (seeders). In this group we could separate some subgroups which are  
315 differentiated by the presence of brachyblasts, because the majority of the  
316 phanerophytes do not have brachyblasts.

317

## 318 Discussion

319 Ecomorphological descriptions and main traits

320 Our results show that this chaparral is composed mainly of phanerophytes,  
321 followed by chamaephytes and amphiphytes. This result is in accordance with  
322 Fernandez-Going et al. (2012), who assert that serpentine soils will have higher  
323 levels of the more stable functional biological types (e.g., perennials), which could  
324 mean chamaephytes and phanerophytes in this case. However, the adaptation to  
325 aridity, low nutrients and heavy metals can inhibit growth of serpentine flora  
326 (Brady et al. 2005; Kazakou et al. 2008; Fernández-Going et al. 2012). These  
327 findings with respect to the biological types, differ from the Mediterranean  
328 serpentine ecosystem of Southern Spain (Hidalgo-Triana 2016, unpublished data),  
329 where the majority of species were chamaephytes. We found these Californian  
330 serpentine plants to be taller and probably more competitive (Cornelissen et al.  
331 2003) than comparable Spanish serpentine plants. The location of renewal buds  
332 was an important character in our analyses since it was the first step of the cluster  
333 and in the PCA. The predominant presence of two biological types chamaephytes  
334 and phanerophytes, could be a strategy that confers to communities of plants the  
335 facility to survive and disperse because renewal buds are allocated in different  
336 places and heights (Cabezudo et al. 2009). However, canopy densities were high

Commented [n13]:

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337 in both ecosystems, showing that the morphology of plants is dwarfed due to the  
338 effect of the serpentine soil.

339 Despite being phanerophytes, 33% of the studied taxa have branches of two  
340 types: dolichoblasts and brachyblast, and with different leaf sizes. Westman  
341 (1981) described the presence of seasonal dimorphism in most plants of the  
342 Californian chaparral. Our results show that a third of the plants have biomass  
343 photosynthetic oscillation throughout the year, which could serve as a mechanism  
344 to avoid water stress during summer drought (Palacio et al. 2004; Palacio and  
345 Montserrat-Martí 2006). Moreover, the studied plants partially shed their leaves in  
346 summer, keeping the dry biomass attached to the body of the plant until they have  
347 the partial shedding.

348 Largely, our results confirm some of the adaptations to the Mediterranean  
349 climate and serpentine soils. One example is the reduced leaf size (Harrison and  
350 Rajakaruna 2011; Anacker et al. 2011). Our study, like other studies on serpentine  
351 ecosystems (Ackerly et al. 2002; Fernández-Goñalons et al. 2012; Adamidis et al.  
352 2014), showed that plants in serpentine have low leaf area. Reduced leaf area is  
353 associated with stress tolerance and promotes nutrient retention, reducing water  
354 loss and susceptibility to desiccation (Mooney and Dunn 1970). Compared to  
355 plants in other Mediterranean ecosystems (Rodríguez-Gallego et al. 2015), like  
356 Spanish *Cistus* shrublands (Pérez Latorre and Cabezudo 2002), leaf sizes in this  
357 study were small, around 14 cm<sup>2</sup>. The coincidence in different Mediterranean non-  
358 serpentine ecosystems could indicate an adaptation to the climate and not to the soil.

359 A large part of the existing literature agrees, in that leaves in serpentine  
360 chaparral are sclerophyllous (Barbour and Major 1977; Kruckeberg 1984, 2006;  
361 Dallman 1998; Sánchez-Mata et al. 2004; Harrison et al. 2006; Alexander et al.  
362 2007; Grace et al. 2007), perhaps in the sense of small, thick and leathery leaves,  
363 as Schimper (1903) pointed out. Nevertheless, in the sense of Orshan (1986),

364 sclerophyllous means leaves that cannot be bent without breaking them.  
365 According to this definition, only 17% of plants in this study had sclerophyllous  
366 leaves, the majority were malacophyllous (61%) or semisclerophyllous (22%).  
367 The dominance of malacophyll species, with non-lignified leaves which last a  
368 year or less, falling at least partially in summer, also constitutes an adaptation to  
369 summer drought. It has been suggested that building sclerophyllous leaves costs  
370 more energy and nutrients to plants and consequently that having malacophyllous  
371 leaves could represent a better strategy for plants growing in nutrient deprived  
372 soils, such as serpentines (Keshet et al. 1990; Pérez Latorre and Cabezudo 2002).

373 Such partial shedding of leaves during summer could promote the  
374 occurrence/spread of fire because of the accumulation of highly flammable  
375 biomass in an ecosystem with a high fire risk (Vogl 1977; Safford and Harrison  
376 2004). Nevertheless, the species studied showed various adaptations to fire.  
377 Several plants showed vegetative regeneration after fire by below ground organs  
378 such as burls (Lloret et al. 1999) which enable the vegetative regeneration of  
379 plants, while some others were seeders: they are cued by fire to reproduce by seed  
380 (Keeley 1992; Safford and Harrison 2004). This ability has also been observed in  
381 heathlands ecosystems in Mediterranean Spain (Pérez Latorre et al. 2007) which  
382 are frequently burned.

383 In relation to the radical system (depth and horizontal development of root  
384 system), many species in Californian chaparral have a dual root system, with a  
385 thick, deep tap root and a mat of fibrous roots closer to the soil surface (Dallman  
386 1998). The majority of the studied plants had only tap roots. Moreover, this type  
387 of root may be adapted to penetrate the hard serpentine rocks diaclasses in the  
388 search for available water. Plants of the serpentine shrublands in Spain show the  
389 same type of root (Hidalgo-Triana 2016, unpublished data). This could be an  
390 ecological adaptation to the aridity of the serpentine soils and to their low content

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391 in essential nutrients (Brady et al. 2005; Kazakou et al. 2008; Harrison and  
392 Rajakaruna 2011). However roots were not very long because serpentine soils are  
393 shallow and rocky.

394

#### 395 Functional groups

396 Our results are consistent with the idea that dry and infertile serpentine soils are  
397 dominated by a mixture of functional groups (as in heathlands; Pérez Latorre et al.  
398 2007). Hobbie et al. (2012) demonstrating that serpentine ecosystems are very  
399 diverse. We obtained the plant functional groups applicable for all the areas where  
400 the NW California's serpentine chaparral is predominant following Sánchez-Mata  
401 and Rodríguez-Rojo (2016).

Commented [n22]:

402 There are few studies using cluster analysis on functional traits (e.g. García-  
403 Mora et al. 1999), and studies for chaparral serpentine ecosystems, are particularly  
404 lacking. The results of our clustering analysis show that the diversity of plant  
405 functional groups in serpentine ecosystems consists of six groups in 18 species,  
406 although two of our groups consisted of only one species, because they did not  
407 share characters with the rest of the species (Pérez Latorre et al. 2007, 2009). We  
408 only sampled the four species of perennial herbs present in the plot, and further  
409 sampling of the rest of the perennial herbs species of the plant community might  
410 increase the functional group diversity types for this ecosystem. In comparison  
411 with other studies in different Mediterranean climate ecosystems, we got the same  
412 number of functional groups but with many fewer studied species: for instance,  
413 the studies by Navarro et al. (2010) in Mediterranean high mountain on the  
414 Moroccan High Atlas, found six groups in 84 studied plants; Grace et al. (2007),  
415 studied functional groups in Californian serpentine communities using  
416 environmental attributes such as climate and geology, and identified 11 floristic

Commented [n23]:

417 groups. In that study, *Heteromeles arbutifolia*, *Adenostoma fasciculatum* and  
418 *Galium andrewsii* were considered in the same group because they shared the  
419 same ecological characteristics; however, in our study they were in different  
420 functional groups according to functional adaptive attributes which are more  
421 predictive to manage ecosystems (Díaz and Cabido 1997). The studied ecosystem  
422 seems to show a high functional diversity and Sri (0.33), and according to the  
423 studies of Grime et al. (2000, 2008) these serpentine ecosystems could be highly  
424 resistant to environmental disturbances.

425 The type of branches of the species was an important characteristic in the  
426 studied plants, especially the presence of only dolichoblasts, only brachyblasts or  
427 of both, which suggests the presence of seasonal dimorphism (Palacio et al. 2004;  
428 Palacio and Montserrat-Martí 2006). On the other hand, species from serpentine  
429 substrates presented a conservative strategy, investing more resources into  
430 structural compounds and thus showing low values of leaf area and leaf thickness  
431 (denser leaves), these characters were used to identify subgroups (Adamidis et al.  
432 2014). Reduced leaf size is an advantage for serpentine plants (Safford et al.  
433 2005). Hairiness or tomentosity showed relative weight because several species  
434 were separated according to that character, which illustrates the degree of  
435 adaptation to minimize the loss of water. This is an advantage in Mediterranean-  
436 climate summer drought (Pérez Latorre and Cabezudo 2002; Pérez Latorre et al.  
437 2007) which could evolve to glabrescence in an evolutive sense doubt to the effect  
438 of the serpentine (serpentine-syndrome, Pichi-Sermolli 1948).

439 Spinescence is a trait that can provide information on drought and grazing  
440 pressure, but studied plants were not spiny. Only *Pickeringia montana* was in the  
441 group with presence of spinescence. This could indicate the absence of long-term  
442 grazing in the ecosystem.

443

444 **Conclusions**

445 The main functional characters of the studied chaparral are the position of the  
446 renewal buds (phanerophytes), a low degree of spinescence, the presence of leaves  
447 in the two types of branches, and mainly malacophyllous leaves, hairy and with  
448 reduced leaf size. The majority of plants shows different strategies of regeneration  
449 after fire, which is an important strategy in worldwide Mediterranean ecosystems,  
450 including Californian.

Commented [n24]:

451 The classification obtained shows that serpentine chaparrals are composed of  
452 species with a wide range of expressions of the functional traits and a high  
453 functional diversity corresponding to a high number of functional groups.  
454 Ecosystems with these traits can present challenges to manage (e.g. fire  
455 management plans, grazing plans, wood harvesting, shrubland management, and  
456 threatened species conservation); but studying the functional groups of the  
457 community, which represents the main functional traits with adaptive meaning,  
458 the management can be simplified. For our work, the 18 species reduced into six  
459 functional groups, which may help simplify land management tasks (Díaz  
460 Barradas et al. 1999; Petchey 2004; Grime et al. 1996) because the species in each  
461 functional group respond to driving environmental conditions in similar fashion  
462 (Walker 1992; Noble and Gitay 1996; Díaz and Cabido 1997).

Commented [n25]:

463 The combination of this study linked to the rest of the ultramafic chaparral in  
464 California, which could have additional functional groups (particularly for  
465 perennial herbs with photosynthetic green part during the summer), could provide  
466 important progress in the management of these kinds of ecosystems. Even the  
467 functional comparison with the already studied (Hidalgo-Triana, 2016,  
468 unpublished data) Spanish and Mediterranean serpentine ecosystems could  
469 provide important management guidelines.

Commented [n26]:

470 It would be interesting to carry out this kind of studies in other serpentine  
471 ecosystems of the world and complete them with more exhaustive studies such as  
472 Gómez-Zotano et al.'s (2014; 2015) classification of serpentine ecosystems of  
473 Spain. The comparison of functional groups among serpentine ecosystems may  
474 distinguish some homogeneous patterns of plant adaptation to serpentine soils  
475 worldwide.

Commented [n27]:

476

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486

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715

716

717 **Electronic Supplementary Material**

718 Appendix S1 1 Phytosociological inventory of the association *Ceanotho albiflori-*  
719 *Quercetum duratae* in the studied plot.

720

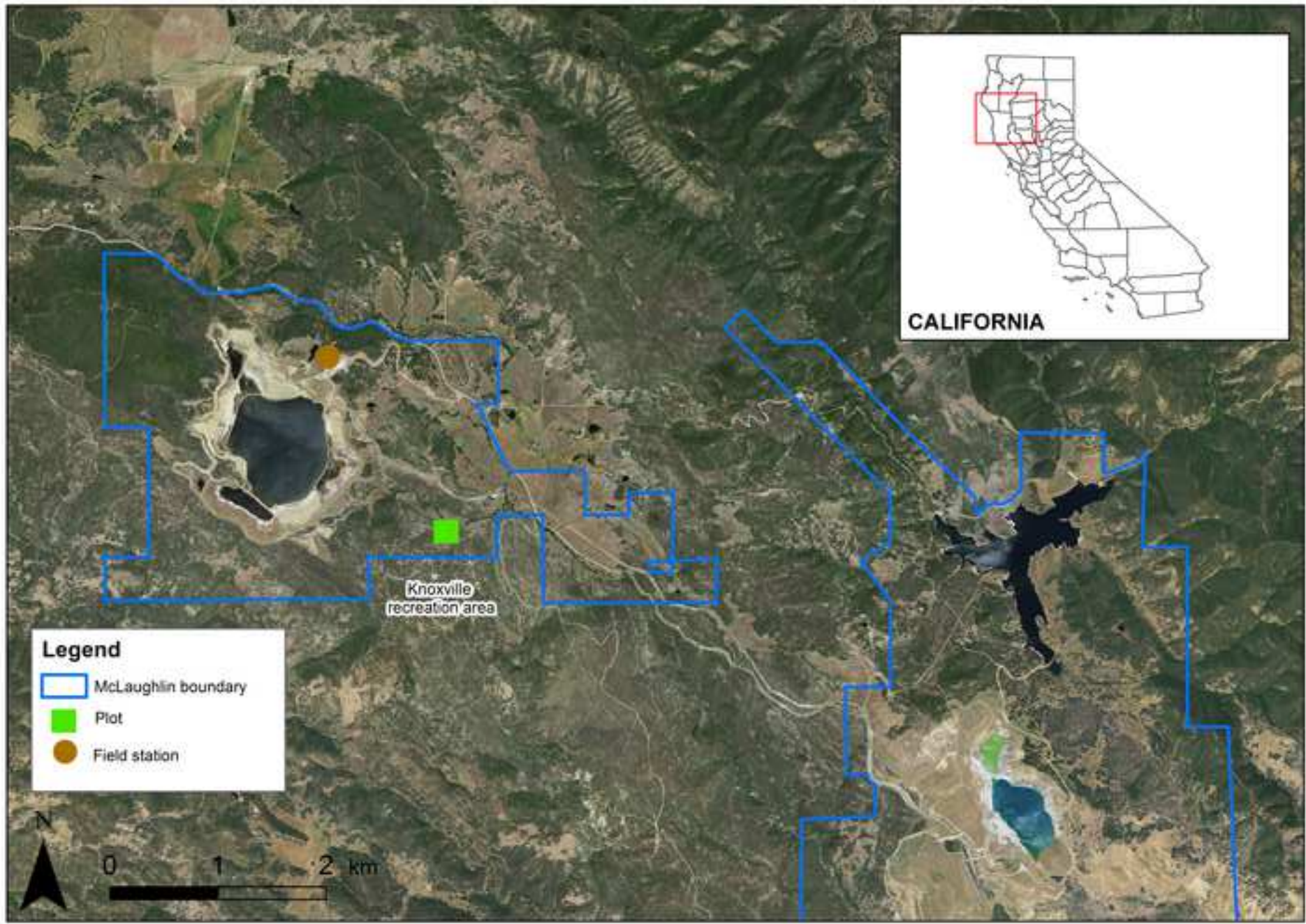
721 Appendix S2 Functional traits with used abbreviations.

722

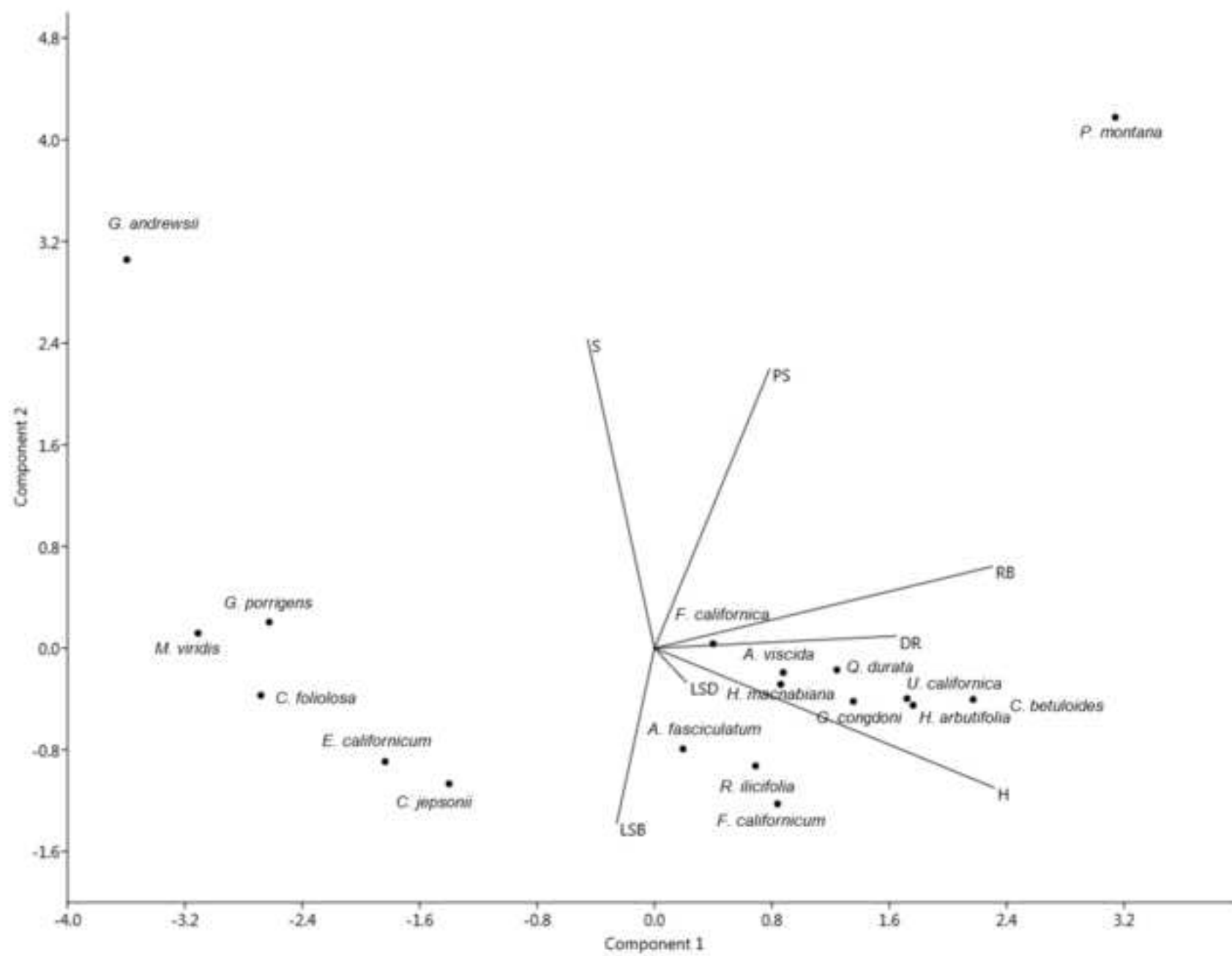
723 Appendix S3 Dendrogram and Table of functional groups.

724

725







**Table 1.** List of studied species, families and serpentine categories (affinity) following Safford et al. (2005).

Studied species	Family	Serpentine affinity
<i>Arctostaphylos viscida</i>	Ericaceae	BE/ WI
<i>Ceanothus jepsonii</i>	Rhamnaceae	SE
<i>Quercus durata</i> var. <i>durata</i>	Fagaceae	SE
<i>Galium porrigens</i>	Rubiaceae	Serpentine and non serpentine
<i>Heteromeles arbutifolia</i>	Rosaceae	Serpentine and non serpentine
<i>Rhamnus ilicifolia</i>	Rhamnaceae	.
<i>Cercocarpus betuloides</i>	Rosaceae	.
<i>Garrya congdonii</i>	Garryaceae	BE
<i>Umbellularia californica</i>	Lauraceae	.
<i>Hesperocyparis macnabiana</i>	Cupresaceae	BE
<i>Eriodictyon californicum</i>	Boraginaceae	.
<i>Adenostoma fasciculatum</i>	Rosaceae	WI/IN
<i>Frangula californica</i>	Rhamnaceae	.
<i>Fremontodendron californicum</i>	Malvaceae	BE/SI
<i>Pickeringia montana</i>	Fabaceae	.
<i>Galium andrewsii</i>	Rubiaceae	SI
<i>Castilleja foliolosa</i>	Orobanchaceae	WI
<i>Monardella viridis</i>	Lamiaceae	BE/SI

SE: strict endemic; BE: broad endemic; BE/SI: broad endemic/strong indicator; SI: strong indicator; WI: weak indicator; WI/IN: weak indicator/indifferent.

Table 2. Traits used in the PCA and in the cluster analysis.

Character	Abreviature	Classes in the matrix
Banch type	BT	0 = Only dolichoblast; 1 = Only brachyblast; 2 = Both types
Depth of root system	DR	0 = <10 cm.; 1 = 10-25 cm.; 2 = 25-50 cm.; 3 = 50-100 cm.; 4 = 1-2 m.; 5 = 2-5 m.; 6 = >5 m.
Crown diameter	CD	0 = ≤10 cm.; 1 = 10-25 cm.; 2 = 25-50 cm.; 3 = 50-100 cm.; 4 = 1-2 m.; 5 = 2-5 m.; 6 = 5-10 m.; 7 = >10 m.
Canopy density	DC	0 = <10 %; 1 = 10-25 %; 2 = 25-50 %; 3 = 50-75 %; 4 = 75-90 %; 5 = >90 %.
Leaf size in cm <sup>2</sup> - larger leaves (dolichoblasts)	LSD	0 = Whithout leaves; 1 = < 0,10 cm <sup>2</sup> ; 2 = 0,10-0,25 cm <sup>2</sup> ; 3 = 0,25-2,25 cm <sup>2</sup> ; 4 = 2,25-12,25 cm <sup>2</sup> ; 5 = 12,25-20,25 cm <sup>2</sup> ; 6 = 20,25-56,25 cm <sup>2</sup> ; 7 = 56,25-180,25 cm <sup>2</sup> ; 8 = 180,25-1640,25 cm <sup>2</sup> ; 9 = >1640,25 cm <sup>2</sup> .
Leaf size in cm <sup>2</sup> - smaller leaves (brachyblasts)	LSB	Idem to LSD
Leaf tomentosity	T	0 = Non hairy leaves; 1 = Leaves with only their lower or upper side hairy; 2 = Hairy leaves on both sides.
Leaf area/Assimilating stem area-ratio	PS	0 = ∞; 1 = ∞ a 1; 2 = 1; 3 = 1-0; 4 = 0.
Location of renewal buds	RB	0 = Th; 1 = Cr; 2 = H; 3 = Ch; 4 = Am, 5 = Ph.
Morphology of aerial part	M	0= Herbaceous scrubs; 1= Woody scrubs; 2= Shrubs; 3= Trees.
Plant height	H	0= ≤10 cm.; 1 =10-25 cm.; 2 = 25-50 cm.; 3 = 50-100 cm; 4 = 1-2 m.; 5 = 2-5 m.; 6 = 5-10 m.; 7 = 10-20 m.; 8 =20-30; 9= >30 m.
Spinescence	S	0 = Absent; 1 = Stems; 2 = Leaves; 3 = Stems and leaves.
Spread of root system	SR	0= <10 cm.; 1= 10-25 cm.; 2 = 25-50 cm.; 3 = 50-100 cm.; 4 = 1-2 m.; 5 = 2-5 m.; 6= >5 m.
Vegetative regeneration after fire	F	0= Plant killed; 1= Plants regenerating from epicormic buds below ground; 2= Plant regenerating from epicormic buds above ground; 3= Plants regenerating from non-epicormic buds below ground; 4=Plants regenerating from non-epicormic buds above ground; 5 = Regeneration by seeds only.



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