Ecol Res (2018) 33: 525–535
DOI 10.1007/s11284-017-1532-6

SPECIAL FEATURE

Ultramafic Ecosystems: Proceedings of the 9th International Conference on Serpentine Ecology

Noelia Hidalgo-Triana · **Andrés Vicente Pérez Latorre**
James Hansen Thorne

Plant functional traits and groups in a Californian serpentine chaparral

Received: 22 July 2017 / Accepted: 14 October 2017 / Published online: 14 November 2017

Abstract 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: *Ceanotho albiflori-Quercetum duratae* 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.

Keywords Ultramafic chaparral · Functional traits · Functional groups · Adaptations · Mediterranean climate

Introduction

Throughout the world, serpentine or ultramafic soils support distinctive vegetation and unique endemic species (Proctor and Woodell 1975; Brooks 1987; Baker et al. 1992; Roberts and Proctor 1992; Kruckeberg 2002). One of the world's richest serpentine floras is found in the Californian Floristic Province (the Mediterranean-climate region encompassing most of California, USA, and small territories in adjacent Oregon and Mexico), which contains at least 246 serpentine endemic plant taxa (Safford et al. 2005). These species are found in a variety of vegetation types including forests, woodlands, sclerophyllous shrublands (“chaparral”) and grasslands (Barbour and Major 1990; Kruckeberg 1984, 2006; Harrison et al. 2006; Alexander Earl et al. 2007; Grace et al. 2007).

We focus on California's serpentine chaparral, a complex of Mediterranean shrub-dominated vegetation types (Anacker et al. 2011) that covers 8.5% of California (Barbour and Major 1990; Keeley and Soderstrom 1986) and consisting of five vegetation types, defined as ‘serpentine or ultramafic chaparrals’. They are considered as xero-edaphic climax vegetation in the phytosociological alliance *Quercion duratae* (*Heteromelo arbutifoliae-Quercetea agrifoliae* class). The floristic structure of this potential vegetation is composed by the leather oak (*Quercus durata*), the dominant character species, and by companion evergreen sclerophyllous shrubs, of which the next most frequent species are from

---

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s11284-017-1532-6) contains supplementary material, which is available to authorized users.

N. Hidalgo-Triana (✉) · A. V. Pérez Latorre
Departamento de Biología Vegetal (Botánica), Facultad de Ciencias,, Universidad de Málaga, 29010 Málaga, Spain
E-mail: nhidalgo@uma.es
Tel.: +34 952131944

J. H. Thorne
Information Center for the Environment Deparment Environmental Science and Policy, University of California, Davis, CA 95616, USA

the genera *Arctostaphylos* and *Ceanothus* (Sánchez-Mata and Rodríguez-Rojo 2016). We focus on one of the types, the interior northwest California serpentine chaparral. Serpentine chaparral has exclusive adaptations to ultramafic soils which have been described generally (Brady et al. 2005; Kazakou et al. 2008).

Ecosystem ecologists have long recognized the functional traits of organisms as key drivers of ecosystem properties (Jones and Lawton 1995). Studies of functional types in relation to climate are common; in the Mediterranean area, they were designed to study how the plants manage to survive in the summer to the typical Mediterranean drought: these are the arid-active species, which still have a photosynthetic green part in the summer and therefore have no choice but to show adaptations to survive which correspond with certain functional types (Evenari et al. 1975; Orshan 1986). However, specific studies on the functional traits of plants in relation to serpentine soils are rare. Some of the general traits identified for serpentine endemics are (Kruckeberg 1984; Brooks 1987; Tibbetts and Smith 1992; Brady et al. 2005): (1) reduced leaf size, for instance lower specific leaf area -SLA- in herbaceous species (Adamidis et al. 2014), and sclerophylly and reduced SLA in serpentine Californian chaparral (Ackerly et al. 2002; Anacker et al. 2011); (2) Leaf succulence (Harrison and Rajakaruna 2011); (3) Smaller stature (Hanes 1981; Kruckeberg 1984; Brooks 1987; Tibbetts and Smith 1992; Brady et al. 2005); (4) Down-regulation of lateral root growth due to the high content in Mg; (5) Slow growth rates (Kruckeberg 1984; Tibbetts and Smith 1992; Brady et al. 2005) and big root (high root biomass or strongly developed root systems; Harrison and Rajakaruna 2011). Finally, with respect to adaptations to fire, serpentine soils can support populations of regionally or locally rare plants that appear to be escaping competition and/or frequent fire (Safford and Harrison 2004).

One of the goals of knowing of the adaptive characters of the components (species) of the ecosystems (Mooney 1974; Le Roux et al. 1984; Pierce 1984) is to detect functional groups of species (FG) (Herrera 1984). Functional groups are sets of plants exhibiting similar responses to environmental conditions and having similar effects on the dominant ecosystem processes (Walker 1992; Noble and Gitay 1996; Díaz and Cabido 1997; Boulangeat et al. 2012). With the help of functional groups we are able to summarize the enormous complexity of individual species and populations into a relatively small number of general recurrent groups (Walker 1992; Grime et al. 1997). This approach is highly relevant to the assessment of ecosystem function (Gitay and Noble 1997) by allowing the generalization of ecosystems to a limited number of functional groups instead of dealing with a large number of species (Grime et al. 1996; Díaz Barradas et al. 1999; Petchey 2004).

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

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

Methods

Study site

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

McLaughlin Reserve has a geological composition predominantly consisting of serpentinite which permitted us to choose a serpentine vegetation plot (20 × 20 m^2), in the Knoxville area located at an altitude of 630 m. (UTM 10S 550179E/4302959 N). The serpentinite mineral group is lizardite, chrysotile and antigorite (University of California and Davis Natural Reserve System 2003). The bioclimatic indexes (*It* and *Io*), based on Rivas-Martínez (1996-2009), were calculated using data from the "Knoxville Creek California station" (38° 51′ 43″/122° 25′ 02″; 670 m) and resulting lower Mesomediterranean bioclimatic belt and ombrotype Subhumid- lower subhumid.

Sampling methods

Vegetation

The sample area was chosen taking into consideration the presence of the characteristic shrub species belonging to the selected chaparral type in a phytosociological sense (Boulangeat et al. 2012). In order to gather vegetation data, a selective plant inventory (Table S1) in the locality was made following Braun-Blanquet instructions (1979), including environmental data, presence and

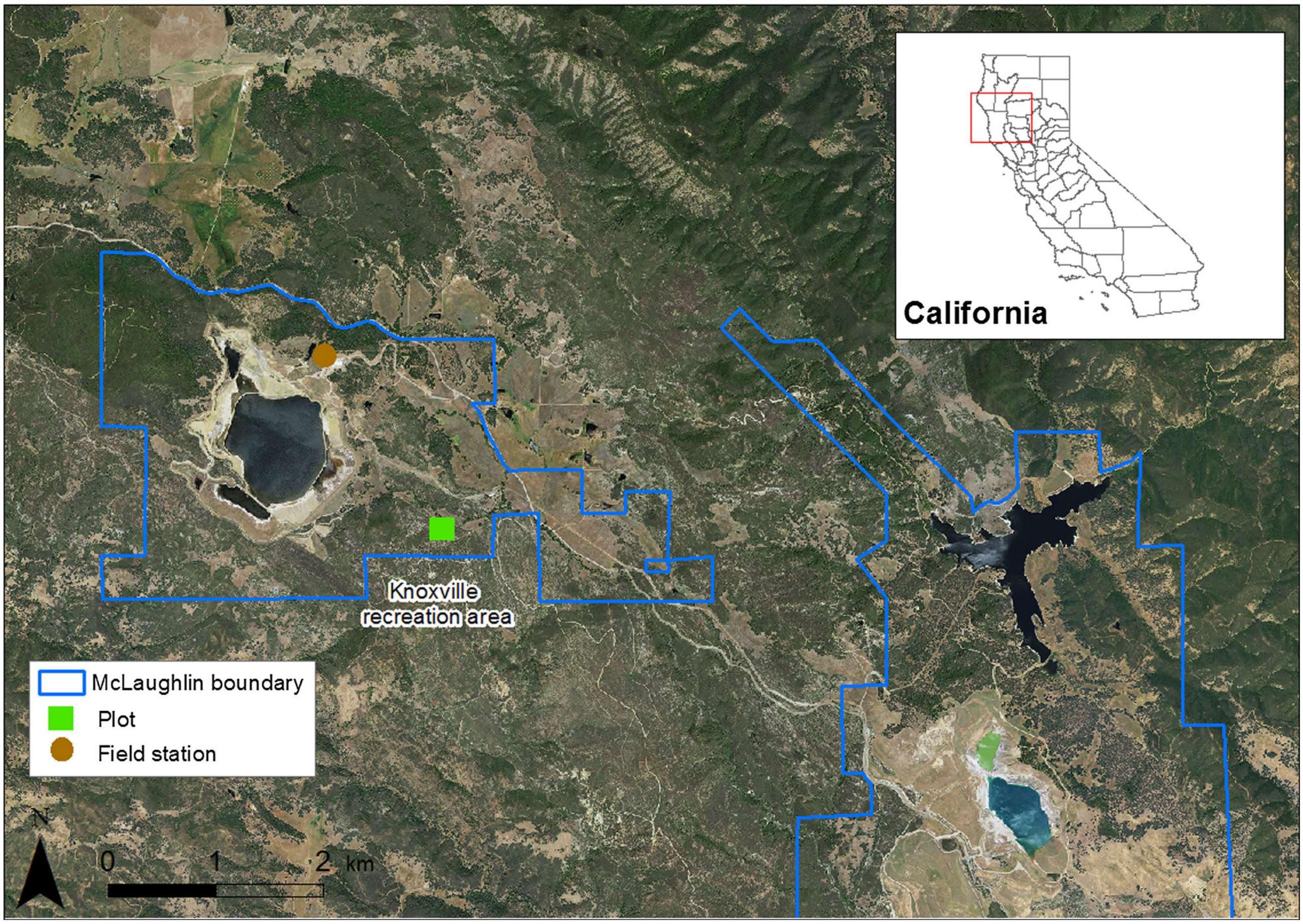

Fig. 1 Location of the study plot in the McLaughlin Reserve (State of California, USA.). The green square is the plot, the brown circle is the field station and blue line is the Reserve boundary. Modified from Farm service agency data

cover of plant species. Among the five vegetation types defined as 'ultramafic chaparrals' in California by Sánchez-Mata and Rodríguez-Rojo (2016), our McLaughlin inventory showed that the study area contains the *Ceanotho albiflori-Quercetum duratae* (chaparral association) Sánchez-Mata, Barbour and Rodríguez-Rojo in Rivas-Martínez 1997 (*Quercion duratae* or *Quercus durata* Alliance by Sawyer et al. (2009), *Adenostomo fasciculatae-Rhamnetalia croceae*, *Heteromelo arbutifoliae-Quercetea agrifoliae*). The area of the selected plot (20 × 20 m^2) exceeds the minimum area necessary to include the theoretical whole diversity of species for shrubland vegetation (Braun-Blanquet 1979; Sawyer et al. 2009; Sánchez-Mata and Rodríguez-Rojo 2016), and for the ultramafic associations. Species were selected from the 20 × 20 m area.

Studied species

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

Ten individuals from each species were measured in the field and voucher specimens from the UC Davis Herbarium were used for laboratory measures. Botanical nomenclature followed mainly Barbour and Major (1990), Baldwin et al. 2012, but further we used USDA Plants Database, Calflora (2016) and the "list of the McLaughlin Reserve plants", unpublished data (2014). Serpentine categories (affinity) following Safford et al. (2005) were indicated for each studied species (Table 1). Voucher specimens of the studied species were stored in the MGC Herbarium (University of Malaga, Spain).

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

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

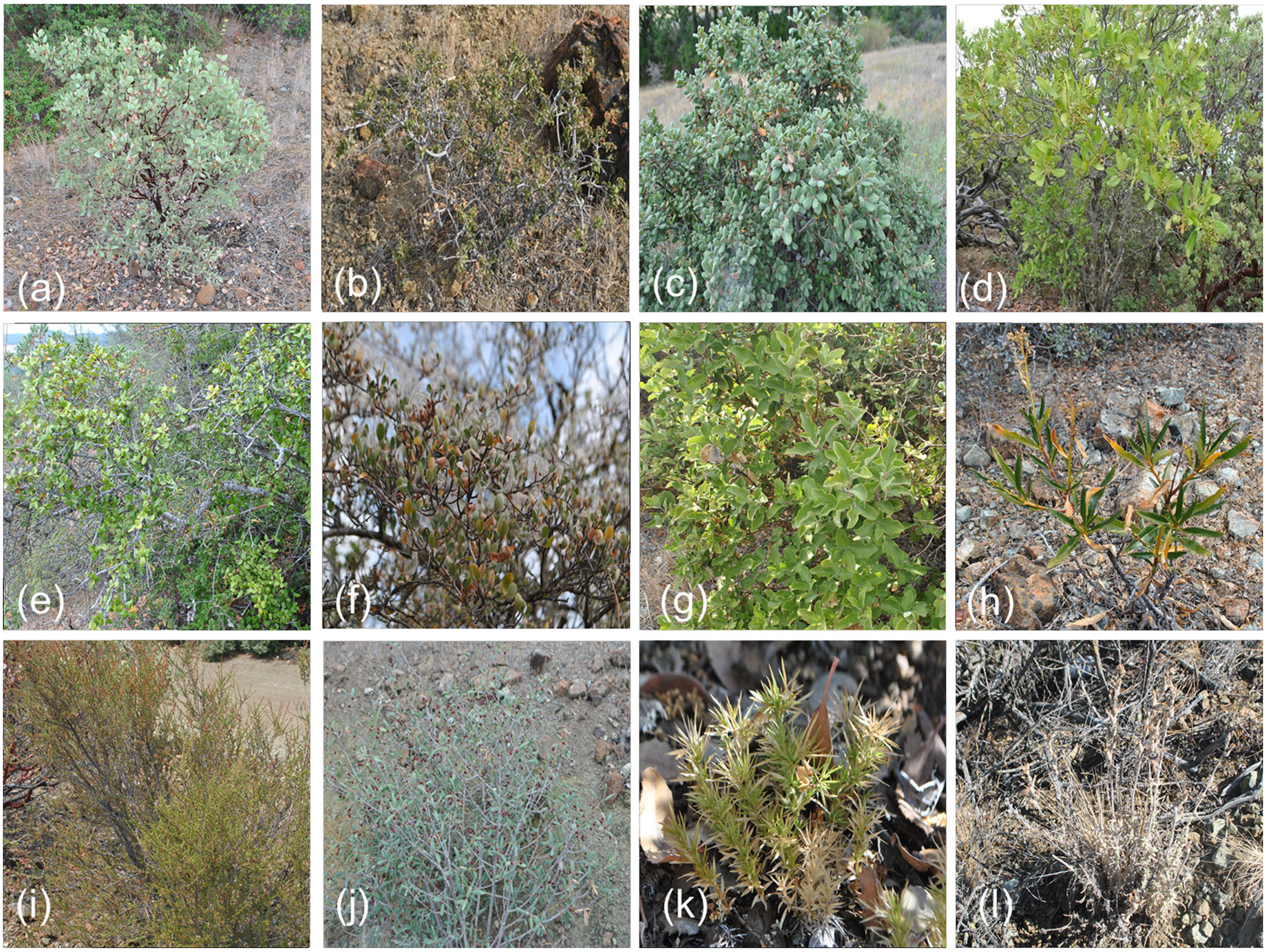

Fig. 2 Photographs of the some species included in this study: **a** *Arctostaphylos viscida*, **b** *Ceanothus jepsonii*, **c** *Quercus durata* var. *durata*, **d** *Heteromeles arbutifolia*, **e** *Rhamnus ilicifolia*, **f** *Cercocarpus betuloides*, **g** *Garrya congdonii*, **h** *Eriodictyon californicum*,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

Studied functional traits (Ecomorphology)

For the ecomorphological characterization of each species, we studied 22 ecomorphological measurable categorical traits using measures developed by Orshan (1982, 1986), Pérez-Latorre and Cabezudo (2002), Cornelissen et al. (2003), and Pérez-Harguindeguy et al. (2013) and using the ecological definitions provided by those authors. The measured traits are described in the ESM1. Some of the main characteristics include: photosynthetic organs (consistency, tomentosity and size); belowground organs (root system); longevity and seasonality; plant regeneration; multiplication and trophism along with fruit type (fleshy, dry); branch type (dolichoblast branches, defined as branches which grow following the annual cycle stretching more than 3 cm and brachyblast branches, defined as branches that show a limited growth each year, remaining as a very short branch state for months or years until they dry out or give rise to vegetative or reproductive dolichoblasts); and the morphology of the aboveground component. For standardization, the methods used for collection of functional traits mainly followed the worldwide handbook for standardized measurement of plant functional traits (Cornelissen et al. 2003; Pérez-Harguindeguy et al. 2013). ESM1 includes descriptions of the methods used for each trait.

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

Statistical analysis

In order to classify the species based on the main measurable characters, a data matrix was built to identify the major axes of variation in the functional traits of the studied species. The trait database was built for all species (18) and with the quantitative and semi-quantitative traits ($n = 14$, Table 2; all of these variables are defined in the ESM1).

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

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

Character	Abbreviation	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^2—larger leaves (dolicoblasts)	LSD	0 = Whithout leaves; 1 = < 0.10 cm^2; 2 = 0.10–0.25 cm^2; 3 = 0.25–2.25 cm^2; 4 = 2.25–12.25 cm^2; 5 = 12.25–20.25 cm^2; 6 = 20.25–56.25 cm^2; 7 = 56.25–180.25 cm^2; 8 = 180.25–1640.25 cm^2; 9 = > 1640.25 cm^2
Leaf size in cm^2—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 = ∞ to 1; 2 = 1; 3 = 1 to 0; 4 = 0
Location of renewal buds	RB	0 = Th (terophytes); 1 = Cr (cryptophytes); 2 = H (hemicryptophytes); 3 = Ch (chamaephytes); 4 = Am (amphiphytes), 5 = Ph (phanerophytes)
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

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

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

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

Results

Ecomorphological description of the community

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

Results of the PCA: main functional traits of serpentine chaparral (characters)

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

Component 1 corresponds with RB, H, DR, and LSD, while component 2 is related to S and PS.

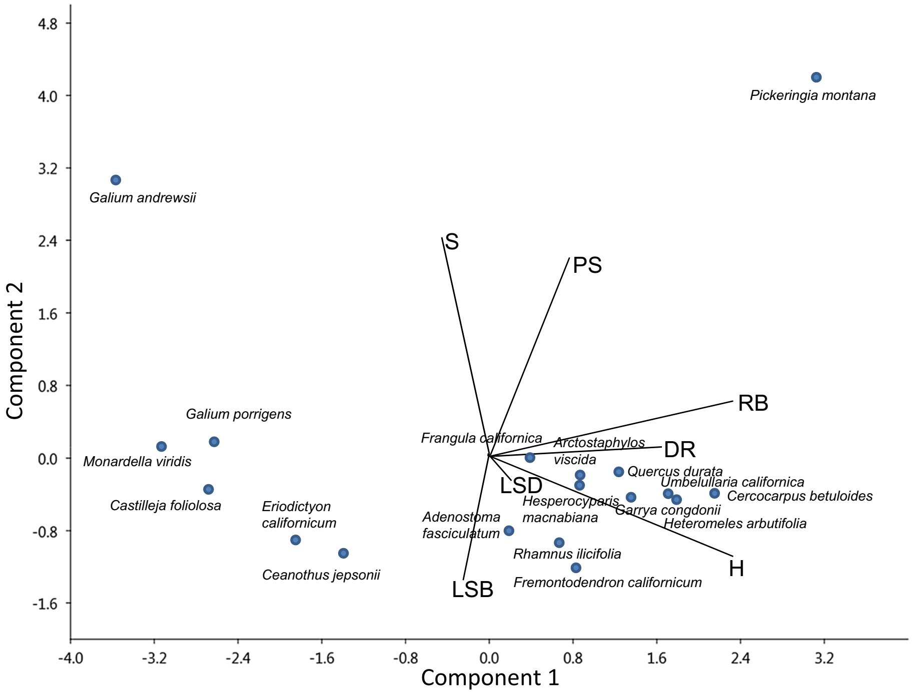

Fig. 3 Biplot spatial diagram with two axes: functional groups based on taxa. Solid black dots are the taxa. Characters are represented using abbreviations in Table 2

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

Our analysis identified six main functional groups (correlation coefficient 0.71; functional groups are shown in the Fig. S1 and Table S2) coexisting in the studied community. The occurrence of six main functional groups (coenomorphs) in a total of 18 species corresponds to a *Sri* of 0.33.

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

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

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

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

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

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

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

Discussion

Ecomorphological descriptions and main traits

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

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

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

A large part of the existing literature agrees, in that leaves in serpentine chaparral are sclerophyllous (Barbour and Major 1990; Kruckeberg 1984; Dallman 1998; Sánchez-Mata et al. 2004; Harrison et al. 2006; Kruckeberg 2006; Alexander Earl et al. 2007; Grace et al. 2007), perhaps in the sense of small, thick and leathery leaves, as Schimper (1903) pointed out. Nevertheless, in the sense of Orshan (1986), sclerophyllous means leaves that cannot be bent without breaking them. According to this definition, only 17% of plants in this study had sclerophyllous leaves, the majority were malacophyllous (61%) or semisclerophyllous (22%). The dominance of malacophyll species, with non-lignified leaves which last a year or less, falling at least partially in summer, also constitutes an adaptation to summer drought. It has been suggested that building sclerophyllous leaves costs more energy and nutrients to plants and consequently that having malacophyllous leaves could represent a better strategy for plants growing in nutrient deprived soils, such as serpentines (Keshet et al. 1990; Pérez-Latorre and Cabezudo 2002).

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

In relation to the radical system (depth and horizontal development of root system), many species in Californian chaparral have a dual root system, with a thick, deep tap root and a mat of fibrous roots closer to the soil surface (Dallman 1998). The majority of the studied plants had only tap roots. Moreover, this type of root may be adapted to penetrate the hard serpentine rocks diaclases in the search for available water. Plants of the serpentine shrublands in Spain show the same type of root (Hidalgo-Triana 2016, unpublished data). This could be an ecological adaptation to the aridity of the serpentine soils and to their low content in essential nutrients (Brady et al. 2005; Kazakou et al. 2008; Harrison and Rajakaruna 2011). However roots were not very long because serpentine soils are shallow and rocky.

Functional groups

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

There are few studies using cluster analysis on functional traits (e.g. García-Mora et al. 1999), and studies for chaparral serpentine ecosystems, are particularly lacking. The results of our clustering analysis show that the diversity of plant functional groups in serpentine ecosystems consists of six groups in 18 species, although two of our groups consisted of only one species, because they did not share characters with the rest of the species (Pérez-Latorre et al. 2007, 2009). We only sampled the four species of perennial herbs present in the plot, and further sampling of the rest of the perennial herbs species of the plant community might increase the functional group diversity types for this ecosystem. In comparison with other studies in different Mediterranean climate ecosystems, we got the same number of functional groups but with many fewer studied species: for instance, the studies by Navarro et al. (2010) in Mediterranean high mountain on the Moroccan High Atlas, found six groups in 84 studied plants; Grace et al. (2007), studied functional groups in Californian serpentine communities using environmental attributes such us climate and geology, and identified 11 floristic groups. In that study, *Heteromeles arbutifolia*, *Adenostoma fasciculatum* and *Galium andrewsii* were considered in the same group because they shared the same ecological characteristics; however, in our study they were in different functional groups according to functional adaptive attributes which are more predictive to manage ecosystems (Díaz and Cabido 1997). The studied ecosystem seems to show a high functional diversity and Sri (0.33), and according to the studies of Grime et al. (2000, 2008) these serpentine ecosystems could be highly resistant to environmental disturbances.

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

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

Conclusions

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

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

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

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

Acknowledgements We gratefully acknowledge the support of the University of Malaga for the stay of N. Hidalgo-Triana in UC Davis, the support of the Department of Environmental Science and Policy of the UC Davis, especially of Jim Quinn, the support of the Centre for Plant Diversity (UC Davis Herbarium), especially Jean Shepard (Collection Manager) and Ellen Dean (Curator), and the support of the McLaughlin Natural Reserve and especially of Catherine Koehler (Resident Director). We gratefully acknowledge Antonio Flores for his help in statistics and Sara Palacio for her corrections.

References

Ackerly D, Knight C, Weiss S, Barton K, Starmer K (2002) Leaf size, specific leaf area and microhabitat distribution of chaparral woody plants: contrasting patterns in species level and community level analyses. Oecologia 130:449–457

Adamidis GC, Kazakou E, Fyllas NM, Panayiotis GD (2014) Species adaptive strategies and leaf economic relationships across serpentine and non-serpentine habitats on Lesbos, eastern Mediterranean. PLoS ONE 9:e96034

Alexander Earl AB, Coleman RG, Keeler-Wolf T, Harrison SP (2007) Serpentine geoecology of western North America: geology, soils and vegetation. Oxford University Press, New York, pp 166–167

Anacker B, Rajakaruna N, Ackerly D, Harrison SP, Keeley J, Vasey M (2011) Ecological strategies in California chaparral: interacting effects of soils, climate, and fire on specific leaf area. Plant Ecol Diversity 4:179–188

Baker AJM, Proctor J, Reeves RD (eds) (1992) The vegetation of ultramafic (serpentine) soils. In: Proceedings of the first international conference on serpentine ecology, Wiley Interscience, University of California, California

Baldwin BG, Goldman D, Keil DJ, Patterson RJ, Rosatti T, Wilken D (2012) The Jepson manual vascular plants of California. University of California Press, Berkeley

Barbour MG, Major J (eds) (1990) California soils and examples of Ultramafic Vegetation. In: Terrestrial vegetation of California, 3rd chapter. Wiley, New York

Boulangeat I, Philippe P, Abdulhak S, Douzet R, Garraud L, Lavergne S, Lavorel S, Vittoz P, Thuiller W (2012) Improving plant functional groups for dynamic models of biodiversity: at the crossroads between functional and community ecology. Glob Change Biol 18:3464–3475

Brady KU, Kruckeberg AR, Bradshaw HD (2005) Evolutionary ecology of plant adaptation to serpentine soils. Annu Rev Ecol Evol Syst 36:243–266

Braun-Blanquet J (1979) Fitosociología. Blume, Madrid

Brooks R (1987) Serpentine and its vegetation. A multidisciplinary approach. Springer, Portland

Cabezudo B, Casimiro-Soriguer Solanas F, Pérez Latorre AV, Dana E, Ramírez J (2009) Hoffmannseggia glauca (Ortega) Einfer (Fabaceae, Caesalpinioideae): nuevo metáfito en el Sur de la Península Ibérica (Málaga, España). Acta Bot Malacitana 34:261–263

Calflora (2016) Information on wild California plants for conservation, education and appreciation. http://www.calflora.org/. Accessed Aug 2016

Cheng W, Coleman DC, Box J (1990) Root dynamics, production and distribution. In: Agroecosystems on the Georgia Piedmont using minirhizotrons. J Appl Ecol 27: 592–604. Rhizosphere Image Gallery: http://ic.ucsc.edu/~wxcheng/wewu/index.html. Accessed Aug 2016

Cornelissen JHC, Lavorel S, Garnier E, Díaz S, Buchmann N, Gurvich DE, Reich PB, ter Steege H, Morgan HD, van der Heijden MGA, Pausas JG, Poorter H (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. Aust J Bot 51:335–380

Dallman PR (1998) Plant life in the world's Mediterranean climates: California, Chile, South Africa, Australia and the Mediterreanean Basin. University of California Press, Sacramento, pp 65–67

Díaz Barradas MC, Zunzunegui M, Tirado R, Ain-Lhout F, García Novo F (1999) Plant functional types and ecosystem function in Mediterranean shrubland. J Veg Sci 10:709–716

Díaz S, Cabido M (1997) Plant functional types and ecosystem function in relation to global change. J Veg Sci 8:463–474

Evenari ME, Schulze D, Kappen L, Buschbom U, Lange OL (1975) Adaptive mechanisms in desert plants. In: Vernberg EJ (ed) Physiological adaptation to the environment. American Institute of Biological Sciences, New York, pp 111–129

Fernandez-Going BM, Anacker BL, Harrison S (2012) Temporal variability in California grasslands: soil type and species functional traits mediate response to precipitation. Ecology 93:14

García-Mora MR, Gallego-Fernández JB, García-Novo F (1999) Plant functional types in coastal foredunes in relation to environmental stress and disturbance. Veg Sci 10:27–34

Gitay H, Noble IR (1997) What are plant functional types and how should we seek them? In: Smith TM, Shygart HH, Woodward FI (eds) Plant functional types. Cambridge University Press, Cambridge, pp 3–19

Gómez-Zotano J, Román-Requena F, Hidalgo-Triana N, Pérez Latorre AV (2014) Biodiversidad y Valores de Conservación de los Ecosistemas Serpentínicos en España: Sierra Bermeja (provincia de Málaga). Boletín de la Asociación de Geógrafos Españoles 65:187–206

Gómez-Zotano J, Román-Requena F, Thorne JH (2015) Attributes and roadblocks: a conservation assessment and policy review of the Sierra Bermeja, a Mediterranean serpentine landscape. Nat Area J 35:328–343

Grace JB, Safford HD, Harrison S (2007) Large-scale causes of variation in the serpentine vegetation of California. Plant Soil 293:121–132

Grime JP, Hodgson JG, Hunt R, Thompson K, Hendry GAF, Campbell BD, Jalili A, Hillier SH, Díaz S, Burke MJW (1996) Functional types: testing the concept in Northern England. In: Smith TM, Shugart HH, Woodward FI (eds) Plant functional types. Cambridge University Press, Cambridge, pp 123–131

Grime JP, Thompson K, Hunt R, Hodgson JG, Cornelissen JHC, Rorison IH, Hendry GAF, Ashenden TW, Askew AP, Band SR, Booth RE, Bossard CC, Campbell BD, Cooper JEL, Davison AW, Gupta PL, Hall W, Hand DW, Hannah MA, Hillier SH, Hodkinson DJ, Jalili A, Liu Z, Mackey JML, Matthews N, Mowforth MA, Neal AM, Reader RJ, Reiling K, Ross-Fraser W, Spencer RE, Sutton F, Tasker DE, Thorpe PC, Whitehouse J (1997) Integrated screening validates primary axes of specialisation in plants. Oikos 79:259–281

Grime JP, Brown VK, Thompson K, Masters GJ, Hillier SH, Clarke IP, Askew AP, Corker D, Kielty P (2000) The response of two contrasting limestone grasslands to stimulated climate change. Science 289:762–765

Grime JP, Fridley JD, Askew AP, Thompson K, Hodgson JG, Bennett CR (2008) Long-term resistance to simulated climate change in an infertile grassland. PNAS 105:10028–10032

Hammer Ø, Harper DAT, Ryan PD (2001) PAST: Paleontological statistics software package for education and data analysis. Palaeontologia Electronica 4, 1–9. PhysicsWeb.http://palaeo-electronica.org/2001_1/past/issue1_01.htm. Accessed Aug 2016

Hanes TL (1981) California chaparral. Mediterranean-types shrublands. Elsevier, Amsterdam, pp 139–174

Harrison S, Rajakaruna N (2011) Serpentine: the evolution and ecology of a model system. University of California Press, Berkeley

Harrison S, Safford HD, Grace JB, Viers JH, Davies KF (2006) Regional and local species richness in an insular environment: serpentine plants in California. Ecol Monogr 76:41–56

Hendrick RL, Pregitzer KS (1992) The demography of fine roots in a northern hardwood forest. Ecology 73: 1994–1104. Rhizosphere Image Gallery. http://ic.ucsc.edu/~wxcheng/wewu/index.html. Accessed Aug 2016

Herrera CM (1984) Tipos morfológicos y funcionales en plantas del matorral mediterráneo del Sur de España. Studia Oecologica 5:7–34

Hidalgo-Triana N (2016) Tipos funcionales (fenomorfología y ecomorfología) de la flora y vegetación serpentinícola mediterránea en Andalucía y California. Dissertation. University of Málaga

Hobbie SE, Jensen DB, Chapin FS (2012) Resource supply and disturbance as controls over present and future plant diversity. In: Schulze ED, Mooney HA (eds) Biodiversity and ecosystem function. Springer, Berlin, pp 385–405

Jones CG, Lawton JH (eds) (1995) Linking species and ecosystems. Springer, New York

Kazakou PG, Dimitrakopoulos B, Reeves RD, Troumbis AY (2008) Hypotheses, mechanisms and trade-offs of tolerance and adaptation to serpentine soils: from species to ecosystem level. E Biol Rev 83(4):495–508

Keeley JE (1992) Recruitment of seedlings and vegetative sprouts in unburned chaparral. Ecology 73:1194–1208

Keeley JE, Soderstrom TJ (1986) Postfire recovery of chaparral along an elevational gradient in southern California. Southwest Natur 31:177–184

Keshet MA, Danin A, Orshan G (1990) Distribution of ecomorphological types along environmental gradients in Israel: 1. Renewal bud location and leaf attributes. Ecol Mediterr 16:151–161

Knoxville Creek California station. PhysicsWeb. http://wrcc.dri.edu/weather/ucmc.html. Accessed Sep 2014

Kruckeberg AR (1984) California serpentines: flora, vegetation, geology, soils, and management problems. University of California Press, Berkeley

Kruckeberg AR (2002) Geology and plant life. University Press, Washington

Kruckeberg AR (2006) Introduction to California soils and plants serpentine, vernal pools, and other geobotanical wonders. University of California Press, Berkeley

Le Roux A, Kyriacou XL, Orshan G (1984) The phenomorphology of selected plants in Mediterranean-type ecosystems of South Africa. Bull Soc Bot Fr 131:441–450

Lloret F, Verdú M, Flores-Hernández N, Valiente Banuet A (1999) Fire and resprouting in Mediterranean ecosystems; insights from an external biogeographical region, the Mexical shrubland. Am J Bot 86:1655–1661

Margaris NS (1981) Adaptive strategies in plants dominating Mediterranean-type ecosystems. In: Specht RL, Di-Castri F, Goodall DW (eds) Mediterranean-type shrublands. Elsevier, Amsterdam, pp 309–315

McCann KS (2000) The diversity-stability debate. Nature 405:228–233

Mooney HA (1974) Plant form as related to environment. Handbook of vegetation science, IV. Junk, Den Haag, pp 111–122

Mooney HA, Dunn EL (1970) Convergent evolution of Mediterranean-climate evergreen sclerophyllous shrubs. Evolution 24:292–303

Navarro T, El Oualidi J, Sghir Taleb M, Pascual V, Cabezudo B, Milla R (2010) Leaf patterns, leaf size and ecologically related traits in high Mediterranean mountain on the Moroccan High Atlas. Plant Ecol 210:275–290

Noble IR, Gitay H (1996) A functional classification for predicting the dynamics of landscapes. J Veg Sci 7:329–336

Orshan G (1982) Monocharacter growth-form types as a tool in an analytic-synthetic study of growth forms in Mediterranean type ecosystems. A proposal for an inter-regional program. Ecol Mediterr 8:159–171

Orshan G (1986) Plant form as describing vegetation and expressing adaptation to environment. Ann Bot 54:7–37

Orshan G (1989) Plant phenomorphological studies in Mediterranean type ecosystems. Kluwer Academic Publishers, Dordrecht

Palacio S, Montserrat-Martí G (2006) Comparison of the bud morphology and shoot growth dynamics of four species of Mediterranean subshrub growing along an altitudinal gradient. Bot J Linn Soc 151:527–539

Palacio S, Milla R, Montserrat-Martí G (2004) Renewal structures and shoot growth of three species of Mediterranean dwarf shrubs growing along an altitudinal gradient. In: Arianoutsou M, Papanastasis V (eds). Proceedings of the 10th MEDECOS Conference. Rhodes, Greece. Millpress Science Publishers. Rotterdam

Pérez Latorre AV, Gavira O, Cabezudo B (2009) Phenomorphology and ecomorphological characters of *Maytenus senegalensis* L. shrublands in the Iberian Peninsula: a comparison with other Mediterranean plant communities. Flora 205:200–210

Pérez-Harguindeguy NA, Díaz S, Garnier E, Lavorel S, Poorter H, Jaureguiberry P, Bret-Harte MS, Cornwell WK, Craine JM, Gurvich DE, Urcelay C, Veneklaas EJ, Reich PB, Poorter L, Wright IJ, Ray P, Enrico L, Pausas GJ, de Vos AC, Buchmann N, Funes G, Quétier F, Hodgson JG, Thompson K, Morgan HD, ter Steege H, van der Heijden MGA, Sack L, Blonder B, Poschlod P, Vaieretti MV, Conti G, Staver AC, Aquino S, Cornelissen JHC (2013) New handbook for standardised measurement of plant functional traits worldwide. Aust J Bot 61:167–234

Pérez-Latorre AV, Cabezudo B (2002) Use of monocharacteristic growth forms and phenological phases to describe and differentiate plant communities in Mediterranean-type ecosystems. Plant Ecol 161:231–249

Pérez-Latorre AV, Gavira O, Cabezudo B (2007) Ecomorphology and phenomorphology of Mediterranean heathlands (SW Iberian Peninsula). Phytocoenologia 37:239–268

Petchey OL (2004) On the statistical significance of functional diversity effects. Funct Ecol 18:297–303

Pichi Sermolli REG (1948) Flora y vegetazione delle serpentini. Webbia 6:1–378

Pierce SM (1984) A synthesis of plant phenology in the fynbos biome. South African National Scientific Programmes Report, 88. Council for Scientific and Industrial Research. Pretoria

Proctor J, Woodell SRJ (1975) The ecology of serpentine soils. Adv Ecol Res 9:255–366

Rivas-Martínez S (1996–2009) Centro de Investigaciones Fitosociológicas. CIF PhysicsWeb. http://www.globalbioclimatics.org. Accessed May 2013

Roberts BA, Proctor J (1992) The ecology of areas with serpentinized rocks. A world view. Kluwer academic publishers, Dordrecht

Rodríguez-Gallego C, Navarro T, Meerts P (2015) A comparative study of leaf trait relationships in coastal dunes in southern Spain. Plant Ecol Evol 148:57–67

Safford H, Harrison H (2004) Fire effects on plant diversity in serpentine vs. sandstone Chaparral. Ecology 85:539–548

Safford H, Viers JH, Harrison SP (2005) Serpentine endemism in the California Flora. A database of serpentine affinity. Madroño 52:222–257

Sánchez-Mata D, Rodríguez-Rojo MP (2016) Mediterranean ultramafic (Serpentine) chaparrals of California (USA): a geobotanical overview. In: Box EO (ed) Vegetation structure and function at multiple spatial, temporal and conceptual scales. Geobotany studies. https://doi.org/10.1007/978-3-319-21452-8_11

Sánchez-Mata D, Rodríguez-Rojo MP, Barbour MG (2004) California ultramafic vegetation: diversity and phytosociological survey. Ultramafic rocks: their soils, vegetation and fauna. Science Reviews, St. Albans, pp 177–181

Sawyer JO, Keeler Wolf T, Evens JM (2009) A manual of California vegetation, 2nd edn. California Native Plant Society, Sacramento

Schimper AFW (1903) Plant geography upon a physiological basis. Clarendon Press, Oxford

Tibbetts RA, Smith JAC (1992) Vacuolar accumulation of calcium and its interaction with magnesium availability. In: The Vegetation of Ultramafic (Serpentine) Soils. Proceedings of the First International Conference on Serpentine Ecology Intercept, Andover, pp 367–73

Tilman D, Downing JA (1994) Biodiversity and stability in grasslands. Nature 367:363–365

University of California, Davis Natural Reserve System (2003) Natural History of the McLaughlin Reserve: Napa, Lake, and Yolo Counties, California, 2nd edn. University of California, Davis

USDA forest service (2016). http://www.fs.fed.us/database/feis/plants/shrub/erical/all.html. Accessed Oct 2016

Vogl RJ (1977) Fire frequency and site degradation. In: Proceedings of the symposium on the environmental consequences of fire and fuel management in mediterranean ecosystems. Usda Forest Service. General Technical Report WO-3, 151–162

Walker BH (1992) Biodiversity and ecological redundancy. Conserv Biol 6:18–23

Westman WE (1981) Seasonal dimorphism of foliage in Californian coastal sage scrub. Oecologia 51:385–388