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SPECIAL FEATURE
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An updated checklist of serpentinophytes for research and conservation in ultramafic ecosystems on the southern Iberian Peninsula (Spain)

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Abstract

Although checklists are essential tools for managing and conserving ultramafic ecosystems, no updated checklist currently exists for ultramafic ecosystems on the southern Iberian Peninsula. Thus, the objectives of our study were (1) to create an updated checklist of serpentinophytes on southern Iberian Peninsula, (2) to determine whether the distribution of serpentinophytes is associated with certain specific types of ultramafic rocks, and (3) to calculate the abundance and richness of serpentinophytes per outcrop to guide conservation efforts. Following a methodology involving field work and searches of bibliographies and herbaria we produced an updated checklist containing 28 serpentinophytes (i.e., 23 obligates, one preferential taxon, one sub-serpentinophyte, and three regional serpentinophytes). The serpentinophytes showed different petrological affinity, where harzburgite–lherzolite and harzburgite–pyroxenite–dunite exhibited higher occupancy, possibly due to their mineralogical and chemical composition (e.g., containing heavy metals) and/or the larger surface area of those outcrops. We also observed that the occupancy of 21 species was higher in different petrographic entities, the reasons for which could be elucidated by future soil analyses. The highest richness of serpentinophytes was found in the main outcrop of Bermeja, followed by smaller outcrops of Alpujata, Aguas, and Guadalhorce Valley. Although the richness of Aguas resembled that of Alpujata, a notable difference emerged in some of its areas owing to bioclimatic and biogeographic isolation. Given the exclusive presence of serpentinophyte flora on the southern Iberian Peninsula, all southern Iberian outcrops should receive some form of conservation as protected natural spaces.

KEYWORDS
conservation, management, petrographic entities, serpentine flora, Sierra Bermeja

1 | INTRODUCTION

Although ultramafic ecosystems appear around the globe, they typically emerge on outcrops scattered as small islands on the Earth's crust (Prance & Brooks, 1988). Serpentine soils, originating from ultramafic rocks, are well known for their physical and chemical anomalies that create an environment hostile to plants (Brooks, 1987; Kruckeberg, 1954). Such anomalies include high Fe and Mg content, low Ca content, a deficiency of nutrients (N, P, and K), infertility, toxic concentrations of heavy metals (e.g., Cr, Ni, Co, Va), extremely slow soil development, and high xerothermicity (Kruckeberg, 1985; López González, 1975; O'Dell et al., 2006; Prance & Brooks, 1988; Whittaker, 1954).

Such characteristics make ultramafic habitats uninhabitable for most plants, and relatively few species, called "serpentinophytes" and described as "serpentinophilous," are adapted to grow on such substrates (Anacker, 2011; Jeffrey, 1987; Pérez-Latorre, Hidalgo-Triana, & Cabezudo, 2013; Rune, 1953; Selvi, 2007). Serpentinophytes, however, are plants adapted to the extreme conditions found in soils developed on ultramafic rocks. Following Kruckeberg (2004), serpentinophytes can be divided into three categories: (a) endemic taxa, linked exclusively to ultramafic substrates; (b) preferential taxa, whose distribution is primarily associated with peridotite but occasionally found on other substrata; and (c) taxa living on both various substrata and on peridotite (i.e., bodenvag taxa). Because significant adaptation to such an isolated lithology is required to survive there, ultramafic ecosystems are centers for plant endemism.

With 123 endemic taxa, the most important area for obligate serpentinophytes in Europe is in the Balkans (Stevanovic et al., 2003; Figure 1a). The westernmost and largest ultramafic peridotite outcrops in the Western Mediterranean Basin are in the southern Iberian Peninsula (Figure 1b), namely in Andalusia, Spain, where they cover a total area of 430 km^2 (IGME, 1970, 1981) and have an altitudinal range of 100–1500 m that spans three bioclimatic belts (Pérez-Latorre et al., 1998).

The flora and plant communities of Andalusian ultramafic ecosystems have been studied by several authors (e.g., Cabezudo et al., 1989; Gálvez Villamuela et al., 2021; López González, 1975; Pérez-Latorre et al., 2018; Pérez-Latorre, Hidalgo Triana, et al., 2013; Pérez-Latorre, Hidalgo-Triana, & Cabezudo, 2013; Rivas Goday, 1974; Rivas & López, 1979). Some species are

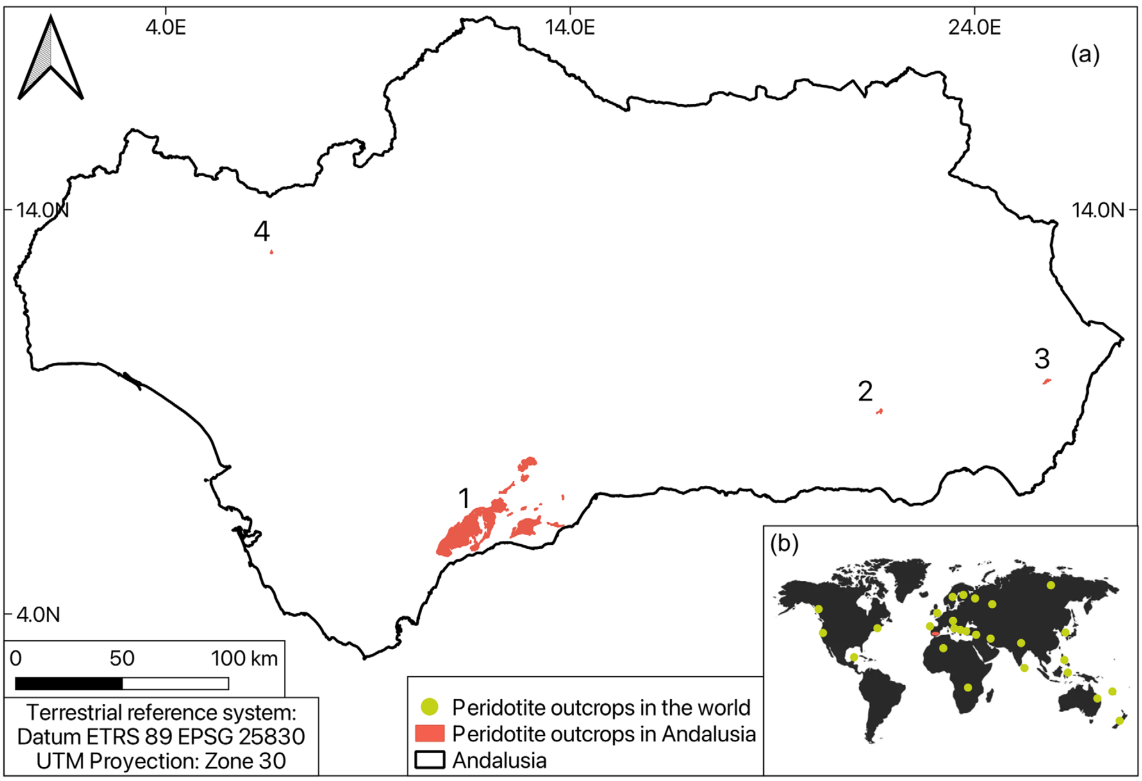

FIGURE 1 (a) Southern Iberian ultramafic outcrops located in Andalusia: (1) Sierra Bermeja, broadly speaking, in Málaga; (2) Sierra Nevada, with Pico del Almirez, in Granada; (3) the Lubrín outcrop in Almería; and (4) the Seville outcrop (i.e., Guillena-El Ronquillo). (b) Global distribution of serpentine ecosystems. *Source*: Data for global general cartography taken from Harrison and Rajakaruna (2011) and for the Andalusian cartography taken from DERA (2021).

hyperaccumulators of Ni (Díez-Garretas et al., 2009; Rufo et al., 2004; van der Ent et al., 2013), whereas others exhibit characteristics of serpentine-morph syndrome (Alados et al., 1999; Hidalgo-Triana & Pérez-Latorre, 2019; López González, 1975).

Within the Western Mediterranean biogeographical subregion lies the southern Iberian Peninsula, for which the most recent checklist of serpentinophytes was published in 2013 and revised in 2018 (Hidalgo Triana & Latorre, 2017; Pérez-Latorre et al., 2018; Pérez-Latorre, Hidalgo-Triana, & Cabezudo, 2013). As of the list's publication and revision, they contain serpentinophytes with different degrees of affinity to ultramafic rocks and can accordingly be divided into three categories (Pérez-Latorre, Hidalgo-Triana, & Cabezudo, 2013): (a) obligates, or plants that strictly inhabit soils over ultramafic rock substrates, which consisted of 24 taxa on the revised list (Pérez-Latorre et al., 2018); (b) preferential taxa, whose distribution of populations is primarily associated with peridotite but which occasionally appear on other substrata and 90% of which are linked to peridotites; and (c) sub-serpentinophytes, whose distribution occurs in peridotite soils but some populations can also be found on other types of soils, with at least 66% of which are linked to ultramafic rocks. According to that categorization, the list contains 28 serpentinophytes: 24 obligates, two preferential taxa, and two sub-serpentinophytes. However, because recent taxonomic and chorological research has furnished new data about southern Iberian serpentine flora, in our work we sought to update the list of serpentinophytes in the southern Iberian Peninsula with reference to the most recent publications and chorological records.

Southern Iberian serpentine flora also grows in different ultramafic massifs that contain different petrographic entities (IGME, 1978; Manteca-Bautista et al., 2022). Together with the presence of heavy metals in the composition of peridotites, the abundance of Mg, and very low amounts of Ca (Morais et al., 2015), another conditioning factor is the mineralogical and lithological difference in the composition of ultramafic rocks. That fact may determine different concentrations of those elements in the soil (Morais et al., 2015) and therefore affect the assembly of plants (Manteca-Bautista et al., 2022) in different ways and can vary the petrological affinity of serpentinophytes. The presence of each heavy metal and variability in the Mg/Ca ratio occurring in southern Iberian ultramafic outcrops contribute to diverse rock types such as dunite, harzburgite–pyroxenite–dunite, harzburgite–lherzolite, pyroxenite, and serpentinite (Manteca-Bautista et al., 2022). Our study also attempted to determine whether the distribution of serpentinophytes is associated with certain specific types of ultramafic rocks.

To date, studies on serpentine flora and its distribution across the different ultramafic rocks have been conducted on an individual serpentinophyte (i.e., *Alyssum serpyllifolium* subsp. *malacitanum*, Manteca-Bautista et al., 2022) but not for the whole group of such plants. In our study, we therefore sought to expand knowledge about the petrological affinity of serpentinophytes, for they may behave differently in different petrological entities.

Considering all of the above, the objectives of our study were:

1. To update the pre-existing list of serpentinophytes in the southern Iberian Peninsula while resolving taxonomic, biological and chorological discrepancies;
2. To determine whether the categories of serpentinophytes on the southern Iberian Peninsula are distributed in association with the different petrographic entities of ultramafic rocks (i.e., dunite, serpentinized facies, harzburgite, harzburgite–dunite, harzburgite–pyroxenite–dunite, harzburgite–lherzolite, lherzolite, undifferentiated peridotite, pyroxenite, and serpentinite) in the ultramafic outcrops there; and
3. To calculate the abundance and richness of serpentinophytes per outcrop to guide conservation efforts in prioritizing outcrops that are richest in serpentinophytes and incrementing protections at the level of taxa and/or the level of natural spaces.

The ultramafic outcrops of the southern Iberian Peninsula provide and a good model for testing our hypothesis that the diverse petrographic entities present in different massifs differ in their richness of serpentinophytes with different degrees of affinity to ultramafic ecosystems.

2 | METHODS

2.1 | Study area

The ultramafic outcrops in the study area are located in the south-eastern part of the Iberian Peninsula, namely in Andalusia, Spain (Figure 1b). They primarily correspond with the provinces of Málaga, with Sierra Bermeja, broadly speaking, as the largest outcrop; Granada, with Pico del Almirez and other minor outcrops in the middle of the Sierra Nevada and Sierra de los Filabres (Granada-Almeria outcrop); and Almería, with the Lubrín outcrop described by Pérez-Latorre, Hidalgo-Triana, and

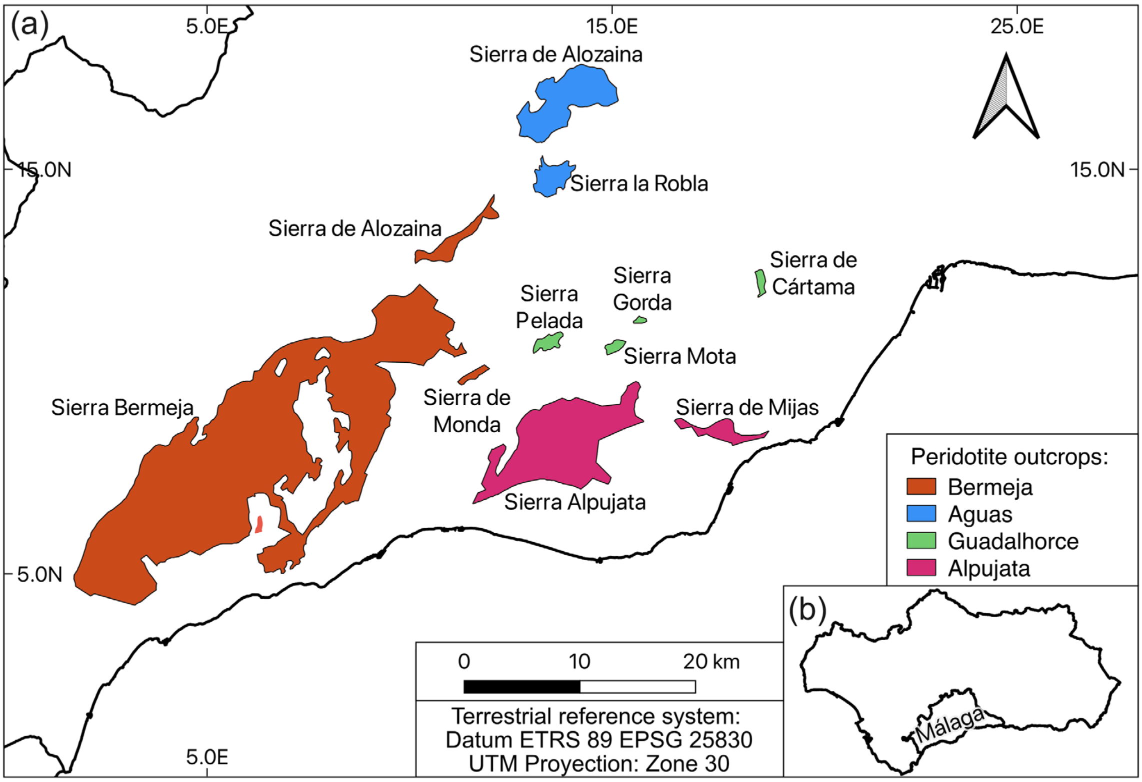

FIGURE 2 (a) Location of the primary ultramafic outcrops in Málaga. (b) Location of Málaga in Andalusia province. *Source*: Data for the general cartography taken from DERA (2021).

Cabezudo (2013) and the Seville outcrop (Guillena-El Ronquillo) described by the IGME (1978).

The largest outcrop, with a total area of 439 km^2, is located in the province of Málaga (Figure 2) and divided into four main outcrops, some of them constituted by different sierras: (1) Bermeja, at 324 km^2 and including the Bermeja, Palmitera, Real, Parda, Monda and Alozaina sierras; (2) Alpujata, at 73 km^2 and including the Alpujata and Mijas sierras; (3) Aguas, at 36 km^2 and including Sierra de Aguas and La Robla sierra; and Guadalhorce Valley, at 6 km^2 and including Pelada, Mota, Gorda, and Cártama sierras. Biogeographically, the outcrops are located in the Palearctic subkingdom, Western Mediterranean subregion, Baetic province, Bermejense sector (Pérez-Latorre et al., 2018; Pérez-Latorre, Hidalgo-Triana, & Cabezudo, 2013).

2.2 | Updated checklist and data provided

To update the pre-existing checklists, we followed the methods established by Pérez-Latorre, Hidalgo-Triana, and Cabezudo (2013) and Pérez-Latorre et al. (2018). First, a new bibliographical search for species cited as possible serpentinophytes was performed (Blanca et al., 2011; Casimiro-Soriguer, 2020; Gálvez Villamuela et al., 2021; Hidalgo-Triana & Pérez-Latorre, 2019), the results of which were supplemented with chorological data obtained from GBIF (2023) and our research team's field work in southern Iberian ultramafic ecosystems. All collected specimens were deposited in the herbarium of the University of Málaga (i.e., MGC Herbarium), and the chorological data for each serpentinophyte, both new and previously described, were updated following our search of the GBIF dataset.

Our research allowed us to create a new classification for endemic serpentinophytes that included the categories of Pérez-Latorre, Hidalgo-Triana, and Cabezudo (2013) and Pérez-Latorre et al. (2018)—obligates, preferential taxa, and sub-serpentinophytes—along with a new category: regional serpentinophytes. The new category comprised plants whose populations on the Iberian Peninsula are overwhelmingly (i.e., 90%) found in serpentine substrates but that can inhabit other types of substrates elsewhere in the world. For taxonomic nomenclature, we adhered primarily to the guidelines provided by the most important floristic works in Southern Iberian Peninsula: Blanca et al. (2011) and Castroviejo (1986–2021), incorporating updates and novelties outlined by Martínez-Flores et al. (2019), Casimiro-Soriguer (2020), Blanca et al. (2021) and Devesa (2023).

For obligate serpentinophytes previously detected by Pérez-Latorre, Hidalgo-Triana, and Cabezudo (2013); Pérez-Latorre, Hidalgo Triana, et al. (2013) and Pérez-Latorre et al. (2018), only new data collected after those publications are provided in this article (e.g., remarks on taxonomic status and chorology).

We also consulted various criteria for each serpentinophyte: taxonomic family; biological type according to Blanca et al. (2011); bioclimatic belt (i.e., thermotype), calculated as a sum of the yearly average temperature, the average minimum temperature of the coldest month of the year, and the average maximum temperature of the coldest month of the year according to REDIAM (2023); ombrotype, according to the ombrotypes map from REDIAM (2023), which is a measure of aridity calculated as the ratio between the yearly positive precipitation and the yearly positive temperature in degrees Celsius (Rivas-Martínez et al., 1997; Torregrosa et al., 2013), and altitudinal range according to DERA (2021), based on the distribution of the entire database with the presence and georeferenced records of the studied serpentinophytes in each shapefile. Descriptive metrics allowed us to analyze the new serpentine checklist in terms of those four criteria. Threatened categories were also added for each serpentinophyte accordingly to the Andalusian Red List (ARD; Cabezudo et al., 2005), along with a protected category according to Andalusian law (i.e., Law 23/2012). Andalusian law includes two means of protection: inclusion on the Andalusian List of Species Under Special Protection (LAERSPE), with species in the category of "in special protection" (RPE), and inclusion in the Andalusian Catalogue of Endangered Species (CAEA). Between the two means, species in the CAEA are more protected—namely, in the categories of "vulnerable" (VU) and "endangered" (EN)—than species on the LAERSPE.

2.3 | Distribution of serpentinophytes per petrographic entity

We used the presence records of each serpentinophyte on our new checklist and from our exploration of the GBIF's (2023) dataset. Each added record was carefully checked, such that a total of 1568 records were depurated and reduced to 997 records in order to avoid toponymy and georeferencing errors. We projected the presence records in the shapefile MAGNA 50 (1:50,000 scale) of the ultramafic outcrops of the province of Málaga elaborated by Manteca-Bautista et al. (2022) containing all petrographic entities present in the ultramafic ecosystem of the study area (Figure S1). According to Manteca-Bautista et al. (2022), the ultramafic petrographic entities presented the following representation in terms of area: harzburgite–lherzolite (180.52 km^2) > harzburgite–pyroxenite–dunite (91.17 km^2) > undifferentiated peridotite (37.75 km^2) > dunite (34.15 km^2) > harzburgite–dunite (24.243 km^2) > serpentinite (21.84 km^2) > serpentinized facies (17.92 km^2) > lherzolite (17.27 km^2) > harzburgite (7.35 km^2) > pyroxenite (3.62 km^2).

We defined occupancy as the total number of sites where the species has been found (Gaston et al., 2000; MacKenzie et al., 2002). To determine whether the categories of serpentinophytes on the southern Iberian Peninsula have a distribution associated with the different petrographic entities of ultramafic rocks, we estimated the occupancy of each category of serpentinophyte (i.e., categorical variable) on each ultramafic petrographic entity (i.e., dunite, serpentinized facies, harzburgite, harzburgite–dunite, harzburgite–pyroxenite–dunite, harzburgite–lherzolite, lherzolite, undifferentiated peridotite, pyroxenite, and serpentinite, categoric variable). We repeated that procedure without considering the category of serpentinophyte affinity in order to evaluate whether the occupancy of each serpentinophyte species varied by petrographic entity. We also elaborated heatmaps for each serpentinophyte using the petrographic entities of the province of Málaga elaborated by Manteca-Bautista et al. (2022).

2.4 | Richness and distribution of serpentinophytes per outcrop

We estimated the richness of serpentinophyte species (i.e., number of serpentinophytes) in each outcrop, which we corrected as a function of the logarithm-adjusted outcrop area (Pérez-García et al., 2012; Pérez-Latorre, Hidalgo-Triana, & Cabezudo, 2013; Whittaker & Fernández-Palacios, 2007). We additionally examined whether the categories of serpentinophytes on the southern Iberian Peninsula have a distribution associated with the different outcrops. To that end, we estimated the occupancy of each category of serpentinophyte (i.e., categorical variable) at each outcrop (i.e., Bermeja, Aguas, Alpujata, and Guadalhorce Valley).

2.5 | Level of environmental protection across the outcrops

We analyzed the threatened and protected status of the serpentinophytes in relation to each outcrop's level of protection by Andalusian law (i.e., DERA, 2021; Andalusian Natural Reserve Network [RENPA], 1989), Spanish law (i.e., MITECO, 2023), or European law (i.e., Council

TABLE 1 Checklist of southern Iberian serpentinophytes, taxonomic authorities, and species attributes.

Taxa	Family	Serpentine affinity
Allium rouyi Gaut.	Alliaceae	Obligate
Alyssum serpyllifolium subsp. *malacitanum* Rivas Goday	Brassicaceae	Obligate
Arenaria capillipes (Boiss.) Boiss.	Caryophyllaceae	Obligate
Armeria colorata Pau	Plumbaginaceae	Obligate
Armeria villosa subsp. *serpentinicola* Cabezudo, Pérez Lat. & Casim.-Sor.Solanas	Plumbaginaceae	Obligate
Bupleurum acutifolium Boiss.	Apiaceae	Obligate
Centaurea carratracensis Lange	Asteraceae	Obligate
Centaurea lainzii Fern. Casas	Asteraceae	Obligate
Cephalaria boetica Boiss.	*Dipsacaceae*	Obligate
Crepis bermejana M.Talavera, C. Sánchez & Talavera	Asteraceae	Obligate
Euphorbia flavicoma subsp. *bermejense* Hidalgo-Triana, Pérez Lat. & Cabezudo	Euphorbiaceae	Obligate
Genista hirsuta subsp. *lanuginosa* (Spach) Nyman	Fabaceae	Obligate
Galatella malacitana Blanca, Gavira & Suár.-Sant.	Asteraceae	Obligate
Iberis fontqueri Pau	Brassicaceae	Obligate
Klasea boetica (DC.) Holub	Asteraceae	Obligate
Linum carratracense (Rivas Goday & Rivas Mart.) Mart.Labarga & Muñoz Garm.	Linaceae	Obligate
Peucedanum officinale L. subsp. *brachyradium*	Apiaceae	Obligate
Saxifraga gemmulosa Boiss.	Saxifragaceae	Obligate
Silene inaperta subsp. *serpentinicola* Talavera	Caryophyllaceae	Obligate
Silene fernandezii Jeanm.	Caryophyllaceae	Obligate
Staehelina baetica DC.	Asteraceae	Obligate
Galium boissierianum (Steud.) Ehrend. & Krendl	Rubiaceae	Obligate
Arenaria retusa Boiss.	Caryophyllaceae	Obligate
Centaurea haenseleri (Boiss.) Boiss.	Asteraceae	Preferential
Galium viridiflorum Boiss. & Reut.	Rubiaceae	Subserpentinophyte
Notholaena marantae (L.) Desv.	Pteridophyte	Regional
Arenaria montana subsp. *montana* var. *glandulosa*	Caryophyllaceae	Regional
Daucus setifolius Desf.	Apiaceae	Regional

Note: Taxonomical family according to Blanca et al. (2011).

Directive 92/43/EEC, 1992), which afforded us information about the conservation management of the ultramafic ecosystems.

3 | RESULTS

3.1 | Updated checklist

Table 1 presents the newly updated checklist of serpentinophytes on the southern Iberian Peninsula with taxonomic authorities, which consists of 23 obligates (82%), one preferential taxon (3.70%), one sub-serpentinophyte (3.70%), and three regional serpentinophytes (10.6%). Among changes on the updated checklist, we added *Arenaria retusa* to the obligate category; transferred *Galium boissieranum* and *Genista hirsuta* subsp. *lanuginosa* from the sub-serpentinophyte and preferential taxa categories, respectively, to the obligate category; transferred *Galium viridiflorum* to the sub-serpentinophyte category; added *Arenaria montana* subsp. *montana* var. *glandulosa* and *Daucus setifolious* to the new created category of regional serpentinophytes; transferred *Notholaena marantae* from the obligate category to the regional serpentinophyte category; and transferred *Centaurea haenseleri* from the obligate category to the preferential taxa category. The updated checklist of serpentinophytes including species attributes is shown in Table S1.

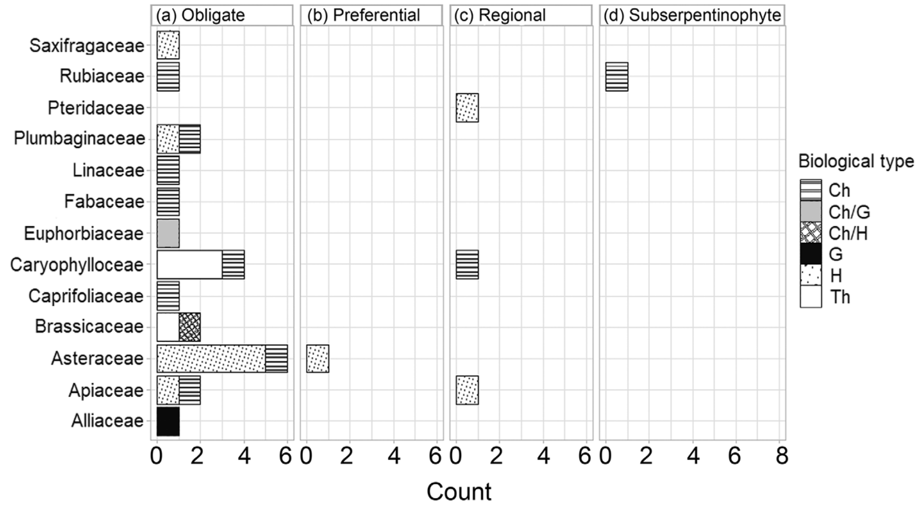

FIGURE 3 Family composition of southern Iberian serpentinophytes and their affinities categories classified by biotype. Affinities categories: (a) obligate, (b) preferential, (c) regional, (d) subserpentinophyte. Biotype: (Th) therophytes, (H) hemicryptophytes, (G) geophytes, and (Ch) chamaephytes.

3.2 | A brief analysis of the serpentinophytes on the southern Iberian Peninsula

The taxonomic spectrum of the obligate serpentinophytes (Table 1) showed the abundance of species in the Asteraceae family (25%), followed by Caryophyllaceae (17.86%) and Apiaceae (10.71%), as shown in Figure 3. The pteridophyte group found representation only in the category of preferential serpentinophytes (i.e., *Notholaena marantae*), the most extensive category around the world. Among other results, our study reveals the absence of gymnosperms as serpentinophytes, despite the presence of certain gymnosperms like *Pinus pinaster* Aiton and *Juniperus oxycedrus* subsp. *oxycedrus* L. being frequently observed in ultramafic outcrops.

Based on occupancy records, the most frequent genera of the studied serpentine flora were *Galium*, *Arenaria*, and *Centaurea*, with 87, 81, and 71 presence records, respectively. The majority of Asteraceae species exhibited the hemicryptophyte biotype, while the Caryophyllaceae species were therophytes and chamaephytes; in general, those three biotypes were the biotypes most represented among the serpentinophytes on the southern Iberian Peninsula (Figure 3). Phanerophytes, by contrast, were non-existent among the southern Iberian serpentinophytes.

Most serpentinophytes presented a wide bioclimatic range, with 17 of 28 taxa (60%) having distribution in two or more bioclimatic belts, namely in the thermo- and meso-Mediterranean belts (Figure 4). A significant portion of the obligate serpentinophytes (i.e., seven taxa) showed a strictly thermophilous distribution with populations distributed only in the thermo-Mediterranean belt: *Allium rouyi*, *Armeria villosa* subsp. *serpentinicola*, *Centaurea carratracensis*, *Euphorbia flavicoma* subsp. *bermejense*, *Galatella malacitana*, *Peucedanum officinale* subsp. *brachyradium*, and *Notholaena marantae*, the last of which is not an obligate but a regional serpentinophyte. Regarding ombrotypes, most of the serpentinophytes (i.e., 16 taxa, approx. 60%), representing

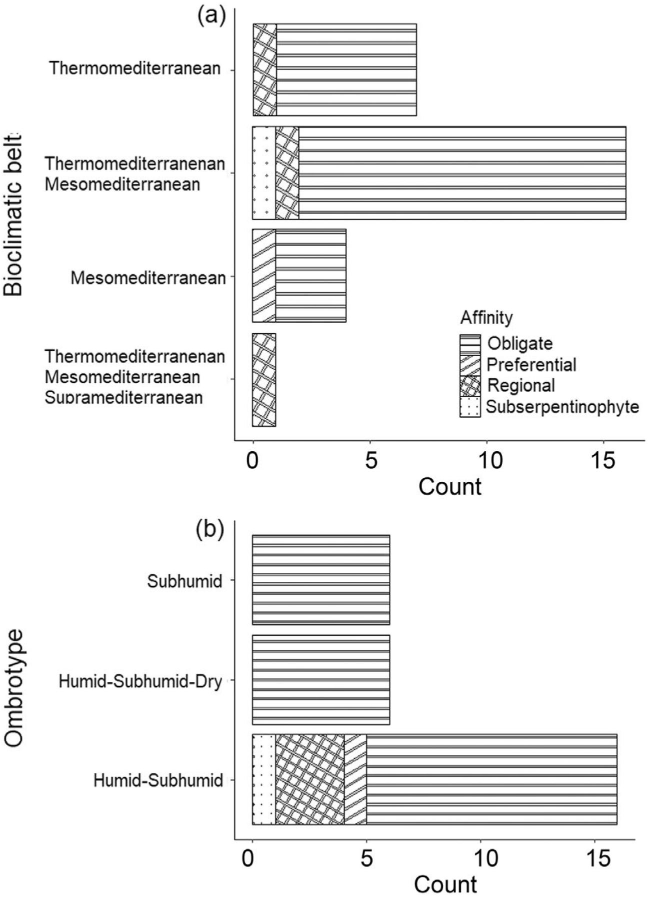

FIGURE 4 Bioclimatic range of southern Iberian serpentinophytes by (a) thermotype (i.e., bioclimatic belts) and (b) ombrotype.

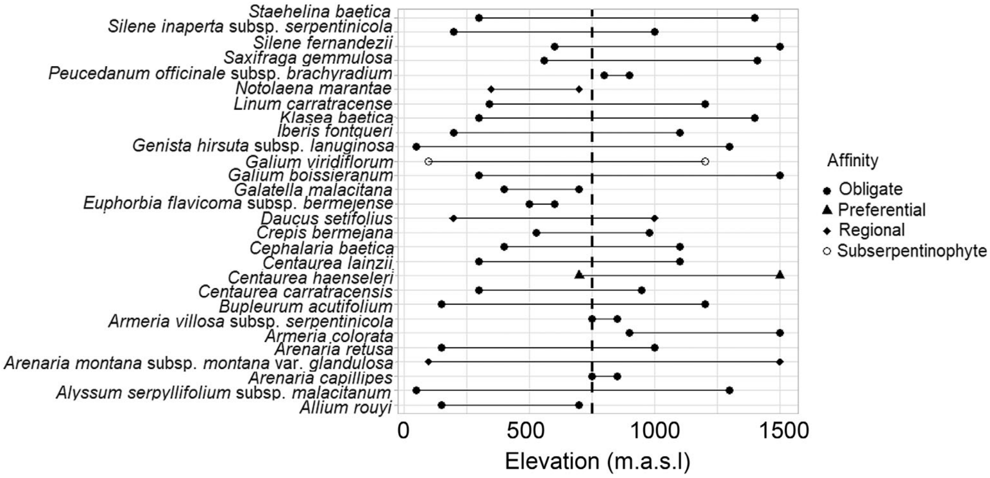

FIGURE 5 Altitudinal range of southern Iberian serpentinophytes, with a black dashed line representing the mean altitudinal range (i.e., 726.37 m.a.s.l.).

all categories of serpentinophytes, showed a massive distribution in the humid or subhumid ombrotype, with a precipitation of 600–1400 mm. Only the obligate serpentinophytes *Allium rouyi*, *Armeria villosa* subsp. *serpentinicola*, *Centaurea carratracensis*, *Euphorbia flavicoma* subsp. *bermejense*, *Galatella malacitana*, and *Peucedanum officinale* subsp. *brachyradium* showed distribution in the subhumid (precipitation = 600–1000 mm) ombrotype, whereas the obligate *Alyssum serpyllifolium* subsp. *malacitanum*, *Arenaria capillipes*, *Genista hirsuta* subsp. *lanuginosa*, *Silene inaperta* subsp. *serpentinicola*, *Staehelina baetica*, and *Galium boissieranum* showed distribution in the humid, subhumid, and dry ombrotypes (Precipitation = 350–1400 mm).

The mean altitudinal position of the serpentinophytes was 726 m.a.s.l. (Figure 5), while the mode was 100–400 m.a.s.l. The obligate serpentinophytes *Galatella malacitana*, *Euphorbia flavicoma* subsp. *bermejense*, and the two species of the genus *Armeria*, together with *Peucedanum officinale* subsp. *brachyradium*, showed a highly restricted altitudinal distribution. Several serpentinophyte species with obligate affinity exhibited a notable altitudinal range, with populations as high as 1400 m.a.s.l. Among those species are *Alyssum serpyllifolium* subsp. *malacitanum*, *Arenaria capillipes*, *Centaurea lainzii*, *Genista hirsuta* subsp. *lanuginosa*, *Klasea baetica*, *Saxifraga gemmulosa*, *Staehelina baetica* and *Galium boissierianum*. Other serpentinophytes with preferential and regional affinity, including *Centaurea haenseleri* and *Arenaria montana* subsp. *montana* var. *glandulosa*, also had populations as high as 1400 m.a.s.l.

The percentage of serpentinophytes threatened according to the ARD (Cabezudo et al., 2005) was 60% (17 taxa, Figure 6, Table S1), 11 taxa of which were included in the two high-risk categories of critically endangered (CR)—namely, *Allium rouyi*, *Centaurea lainzii*, and *Peucedanum officinale* subsp. *brachyradium*,or endangered (EN)—namely, *Armeria colorata*, *Armeria villosa* subsp. *serpentinicola*, *Centaurea carratracensis*, *Cephalaria boetica*, *Klasea baetica*, *Silene inaperta* subsp. *serpentinicola*, *Silene fernandezii*, and *Centaurea haenseleri*. Six taxa were classified as vulnerable (VU): *Bupleurum acutifolium*, *Crepis bermejana*, *Iberis fontqueri*, *Saxifraga gemmulosa*, *Galium boissieranum*, and *Galium viridiflorum* (Figure 6, Table S1). However, in terms of serpentinophytes protected by Andalusian legislation (Decreto 23/2012), only some of those obligate serpentinophytes (<30%) have been protected with VU status (i.e., included in the CAEA, Decreto 23/2012) or RPE status (i.e., included in the LAERSPE, Decreto 23/2012), and only the sub-serpentinophyte *Galium viridiflorum* is a non-obligate serpentinophyte within the RPE protection category. It is worth noting that none of the serpentinophytes are legally protected within the highest category of protection (i.e., EN). Representative images of several serpentinophytes taxa are shown in Figures 7 and 8, where taxa with threat categories (EN) and (VU) included in the Andalusian Red List are indicated.

3.3 | Distribution of serpentinophytes across petrographic entities

3.3.1 | Serpentinophytes with different levels of affinity to petrographic entities

The harzburgite–lherzolite and harzburgite–pyroxenite–dunite entities were the entities with the most records (i.e., specimens collected in herbaria), with 222 and 205 records, respectively, followed by undifferentiated peridotites, harzburgite–dunite, and dunite with 36, 33, and 32 records, respectively (Table 2). When we examined the serpentinophytes' affinity to petrographic entities, we observed that the affinities of the southern

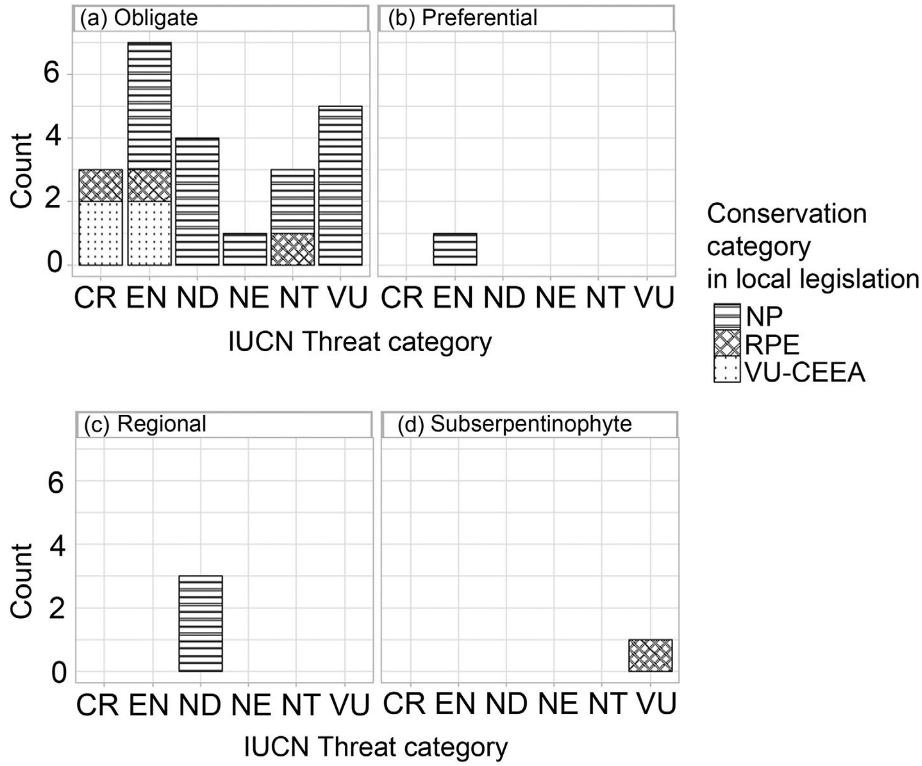

FIGURE 6 Threatened and protected statuses of southern Iberian serpentinophytes and their affinities categories. Affinities categories: (a) obligate, (b) preferential, (c) regional, and (d) subserpentinophyte. Threatened status by local legislation: (NP) non-protected, (RPE) under a special regime of protection, (VU-CEEA) vulnerable by Spanish catalogue of threatened species. IUCN categories: (VU) vulnerable, (CR) critically endangered, (EN) endangered, (NT) near threatened, (NE) not evaluated.

Iberian serpentinophytes varied across all petrographic entities except for serpentinized facies (Table 2, Figure 9). The petrographic entities with the majority of records across all serpentinophytes categories were harzburgite–lherzolite, followed by harzburgite–pyroxenite–dunite (Figure 9, Table 2). These entities also have the highest surface areas (180.52 and 91.8 km^2, respectively). Serpentinophytes from the sub-serpentinophyte category presented the majority of records in the harzburgite–pyroxenite–dunite entity, while the rest of categories presented the majority of records in the harzburgite–lherzolite entity. The trend of affinity for the obligates was harzburgite–lherzolite > harzburgite–dunite–pyroxenite > harzburgite–dunite–undifferentiated peridotite > dunite > serpentinite > lherzolite > harzburgite > pyroxenite; for the preferential taxa was harzburgite–lherzolite > harzburgite–pyroxenite–dunite; for the sub-serpentinophytes was harzburgite–pyroxenite–dunite > harzburgite–lherzolite; and for the regional serpentinophytes was harzburgite–lherzolite > harzburgite–pyroxenite–dunite > harzburgite dunite > dunite, which showed the same tendency as the obligates.

3.4 | Serpentinophyte species per petrographic entity

Twenty-one species showed higher presence records across distinct petrographic entities (Figures 10 and S2–S6): 18 obligates (i.e., *Allium rouyi*, *Alyssum serpyllifolium* subsp. *malacitanum*, *Crepis bermejana*, *Centaurea carratracensis*, *Klasea baetica*, *Linum carratracense*, *Galatella malacitana*, *Genista hirsuta* subsp. *lanuginosa*, *Saxifraga gemmulosa*, *Silene fernandezii*, *Staehelina baetica*, and *Arenaria retusa*), one regional serpentinophyte (i.e., *Arenaria montana* subsp. *montana* var. *glandulosa*), and one sub-serpentinophyte (i.e., *Galium viridiflorum*), as detailed in Table S2.

3.5 | Richness and distribution of serpentinophytes by outcrop

3.5.1 | Richness of serpentinophytes per outcrop

Without distinction between the categories of serpentinophytes, the greatest richness of serpentinophytes emerged in the main outcrop of Bermeja, which had 26 of the 28 total serpentinophytes. The Alpujata and Sierra de Aguas outcrops clearly exhibit levels of species richness comparable to Bermeja's despite their smaller sizes (Table 3). Furthermore, the Bermeja outcrop, the largest one in the study area, hosted five plants that are strictly endemic to the area (i.e., *Allium rouyi*, *Arenaria capillipes*, *Armeria colorata*, *Euphorbia flavicoma* subsp. *bermejense*, and *Peucedanum officinale* subsp.

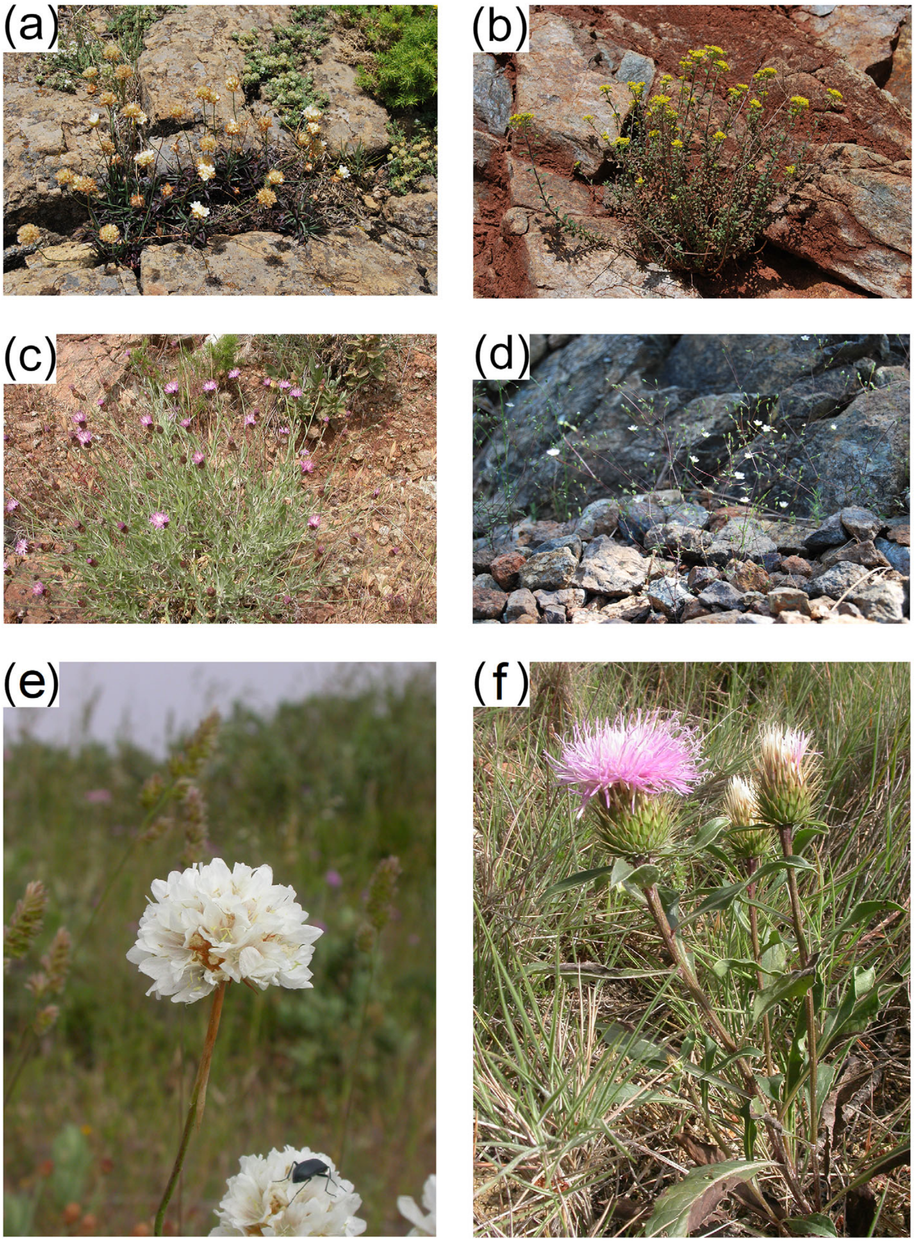

FIGURE 7 Representative images of serpentinophyte taxa identified in ultramafic ecosystems within the study area. (a) **Armeria colorata* (Plumbaginaceae), (b) *Alyssum serpyllifolium* subsp. *malacitanum* (Brassicaceae), (c) **Centaurea carratracensis* (Asteraceae), (d) *Arenaria capillipes* (Caryophyllaceae), (e) **Armeria villosa* subsp. *serpentinicola* (Plumbaginaceae), (f) **Klasea baetica* (Asteraceae). Taxa classified as endangered (EN) in the Andalusian Red List are marked with an asterisk (*). (Photographs: A.V. Pérez-Latorre).

brachyradium), while Sierra de Aguas, the outcrop located further north, boasts *Centaurea carratracensis* and *A. villosa* subsp. *serpentinicola* as species strictly endemic to that site.

Additionally, the Bermeja outcrop was the most diverse in terms of the serpentinophytes present, including serpentinophytes belonging to all four categories: obligate, preferential, regional, and sub-serpentinophyte (Figure 11). However, the Aguas and Alpujata outcrops showed a high presence of the three categories of obligate, regional, and sub-serpentinophytes, while the Guadalhorce Valley outcrop—the smallest outcrop—presented only one obligate and one regional serpentinophyte (Figure 11).

3.6 | Distribution of serpentinophytes by outcrop and affinity category

The outcrops with the most records were Bermeja and Aguas, with 414 and 94 records, respectively (Table 4). Additionally, Bermeja was the only outcrop with presence records of preferential serpentinophytes.

3.7 | Levels of environmental protection across the outcrops

All of the outcrops have some portion of their territories designated as Biosphere Reserves and are

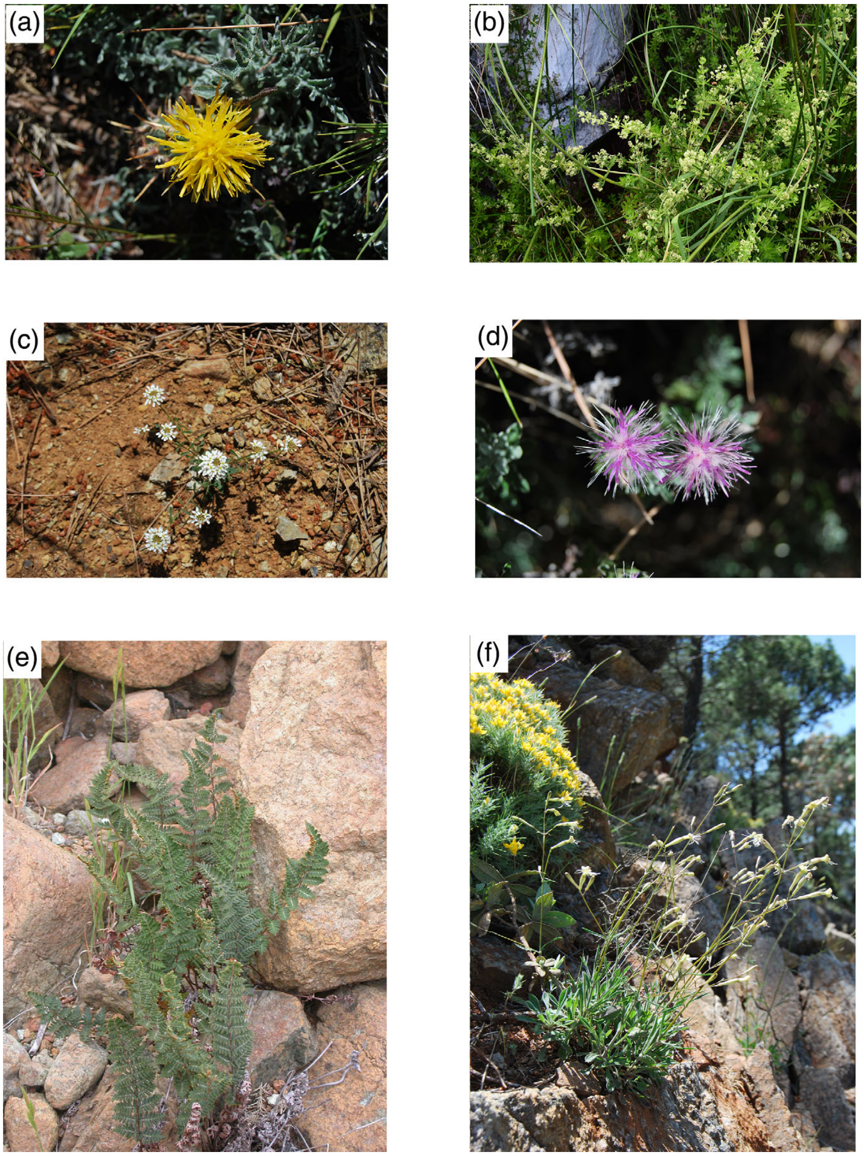

FIGURE 8 Representative images of serpentinophyte taxa identified in ultramafic ecosystems within the study area. (a) ***Centaurea haenseleri* (Asteraceae), (b) **Galium viridiflorum* (Rubiaceae), (c) **Iberis fontqueri* (Brassicaceae), (d) *Staehelina baetica* (Asteraceae), (e) *Notholaena marantae* (Pteridaceae), (f) ***Silene fernandezii* (Caryophyllaceae). Taxa classified in the Andalusian Red List as vulnerable (VU) are marked with an asterisk (*) and the endangered (EN) with two (**). (Photographs: A.V. Pérez-Latorre).

TABLE 2 Number of serpentinophytes by category of serpentinophytes in terms of number of presence records in the different petrographic entities (*).

Petrographic entity	Area (km^2)	O	P	R	S	Total of records
Harzburgite-Lherzolite	180.52	189	14	14	5	222
Harzburgite-Dunite pyroxenite	91.17	172	8	10	15	205
Undifferentiated peridotite	37.75	30	0	4	2	36
Dunite	34.15	25	1	4	2	32
Harzburgite-Dunite	24.24	26	0	5	2	33
Serpentinites	21.84	19	0	3	1	23
Serpentinized facies	17.92	8	0	2	3	13
Lherzolite	17.27	14	0	2	0	16
Harzburgite	7.35	13	0	0	1	14
Pyroxenite	3.62	4	0	0	0	4

Abbreviations: O, obligate; P, preferential; R, regional; S, subserpentinophyte.

included in the World Network of Biosphere Reserves, an international means of protection designed by the UNESCO (Figure 12). The other types of sites present in the study area are twofold: Natura 2000 sites designated under the EU Habitats Directive as Special Areas of Conservation (SACs) and other natural spaces

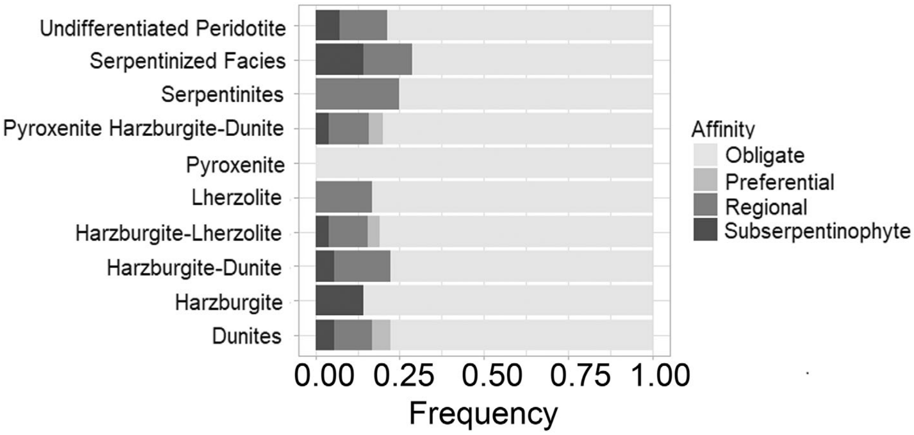

FIGURE 9 Proportion of records of southern Iberian serpentinophytes for each petrographic entity.

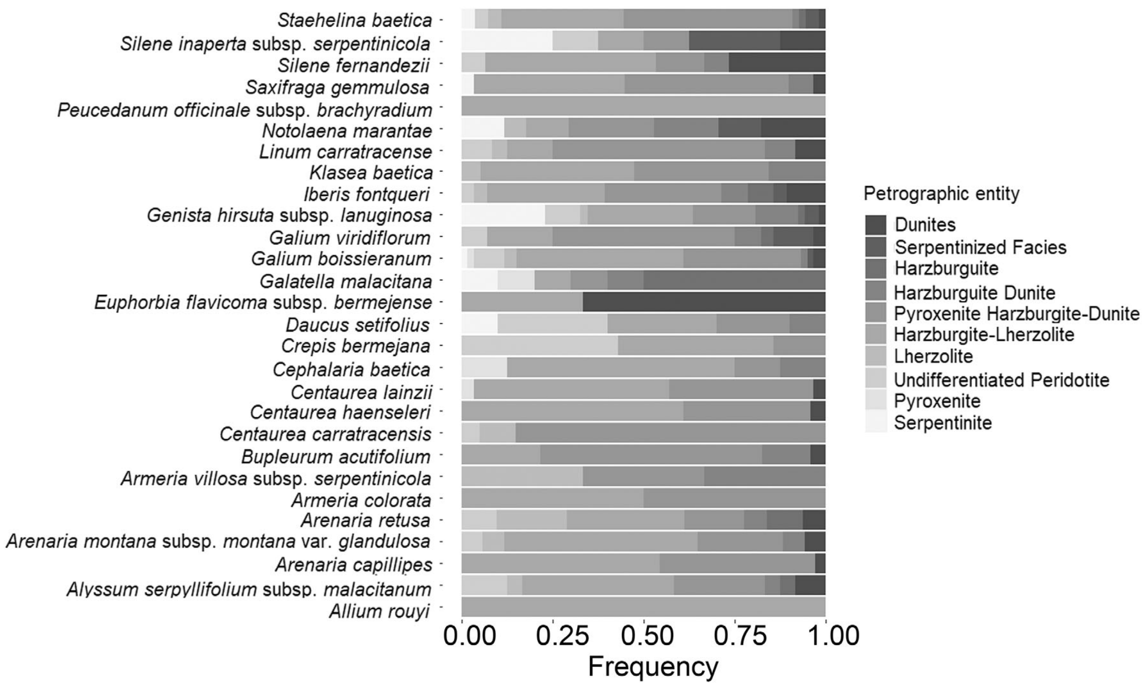

FIGURE 10 Proportion of records for each southern Iberian serpentinophyte per outcrop.

TABLE 3 Values of richness (i.e., number of serpentinophytes) and corrected richness (i.e., number of serpentinophytes) per outcrop (i.e., area) with the log-corrected area estimated using the formula richness/Ln (area).

Outcrop	Area (km^2)	Richness	Corrected richness
Bermeja	324	26	4.49
Alpujata	73	18	4.19
Aguas	36	15	4.18
Guadalhorce	6	2	1.11

protected by the Andalusian government and included in RENPA.

The Aguas and Alpujata outcrops contain SACs; however, in the case of Alpujata, its SACs are associated with rivers, not the presence of the ultramafic outcrop or ecosystems. Even so, it is important to highlight the presence of the endemic serpentinophytes *Armeria villosa* subsp. *serpentinicola* and *Centaurea carratracensis*, both

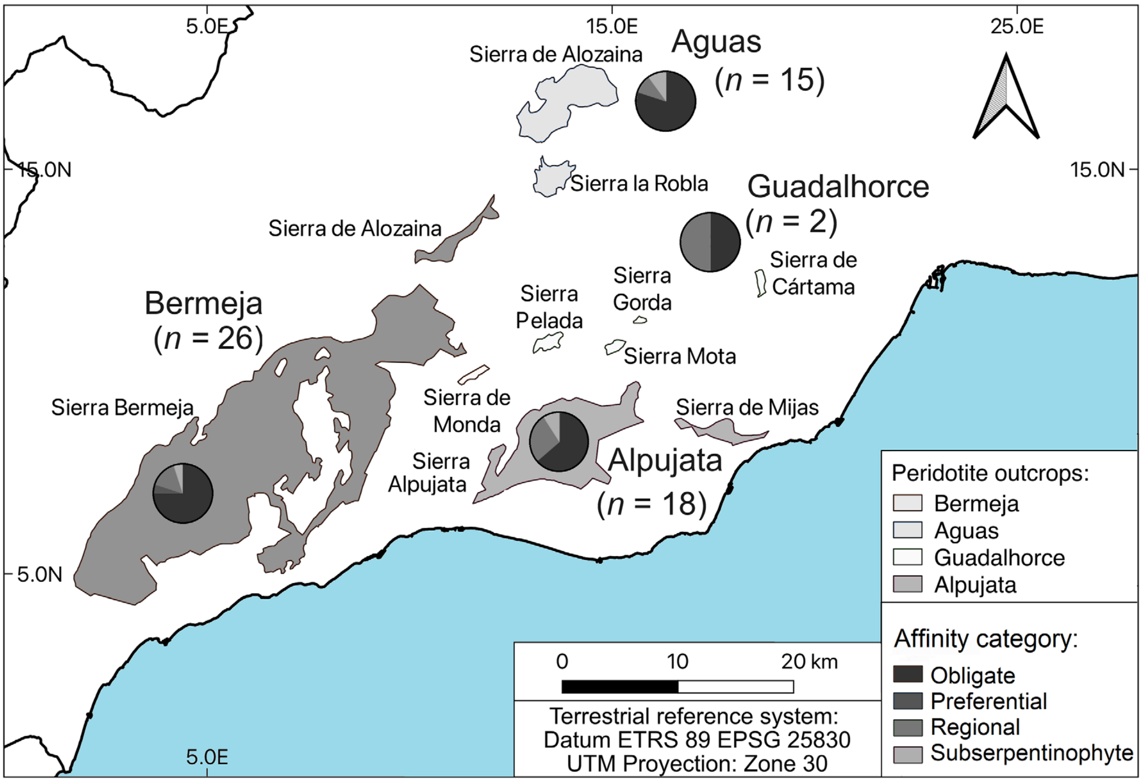

FIGURE 11 Map of four main outcrops and their composition in terms of number of southern Iberian serpentinophyte species and their affinity, in which represents the number of serpentinophyte species per outcrop.

TABLE 4 Number of presence records of serpentinophytes species and their affinity categories in the different outcrops.

Outcrop	Total of records	O	P	R	S
Bermeja	414	341	23	30	20
Alpujata	88	72	0	10	6
Aguas	94	86	0	3	5
Guadalhorce	2	1	0	1	0

Abbreviations: O, obligate; P, preferential; R, regional; S, subserpentinophyte.

included in the ARD, and *Armeria villosa* subsp. *serpentinicola*, protected by Andalusian law (i.e., Law 23/2012) and restricted to the Aguas outcrop.

However, the Guadalhorce Valley outcrop, including the isolated outcrop of Sierra de Mijas, lacks any form of protection designation even though it coincides with the presence of a few endemic species, including the only occurrence of *Silene inaperta* subsp. *serpentinicola*, included in the ARD.

The Bermeja outcrop stands out as the only outcrop with approximately 50% of its area protected by RENPA, namely the National Park Sierra de las Nieves and Natural Site of Sierra Bermeja, although the designation of Natural Site is one of the least restrictive in terms of protection, while the Natural Site designation protects only the *Abies pinsapo* forest and surroundings (Figure 12). The rest of the Bermeja outcrop lacks protection, despite having the most serpentinophytes and presenting five restrictive endemic serpentinophytes without records of presence in the other ultramafic outcrops (i.e., *Allium rouyi*, *Arenaria capillipes*, *Armeria colorata*, *Euphorbia flavicoma* subsp. *bermejense*, and *Peucedanum officinale* subsp. *brachyradium*). Some areas of the Bermeja outcrop and the other outcrops, primarily Alpujata and Guadalhorce Valley, lack such comprehensive protection and are only designated as SACs along their riverbeds, while their serpentinite-rich soils remain largely unprotected (Figure 12).

4 | DISCUSSION

4.1 | The updated checklist of serpentinophytes for the southern area of the Iberian Peninsula

The newly updated checklist for the southern area of the Iberian Peninsula consisted of a total of 28 serpentinophytes, categorized in the three pre-existing categories indicated by Pérez-Latorre, Hidalgo-Triana, and

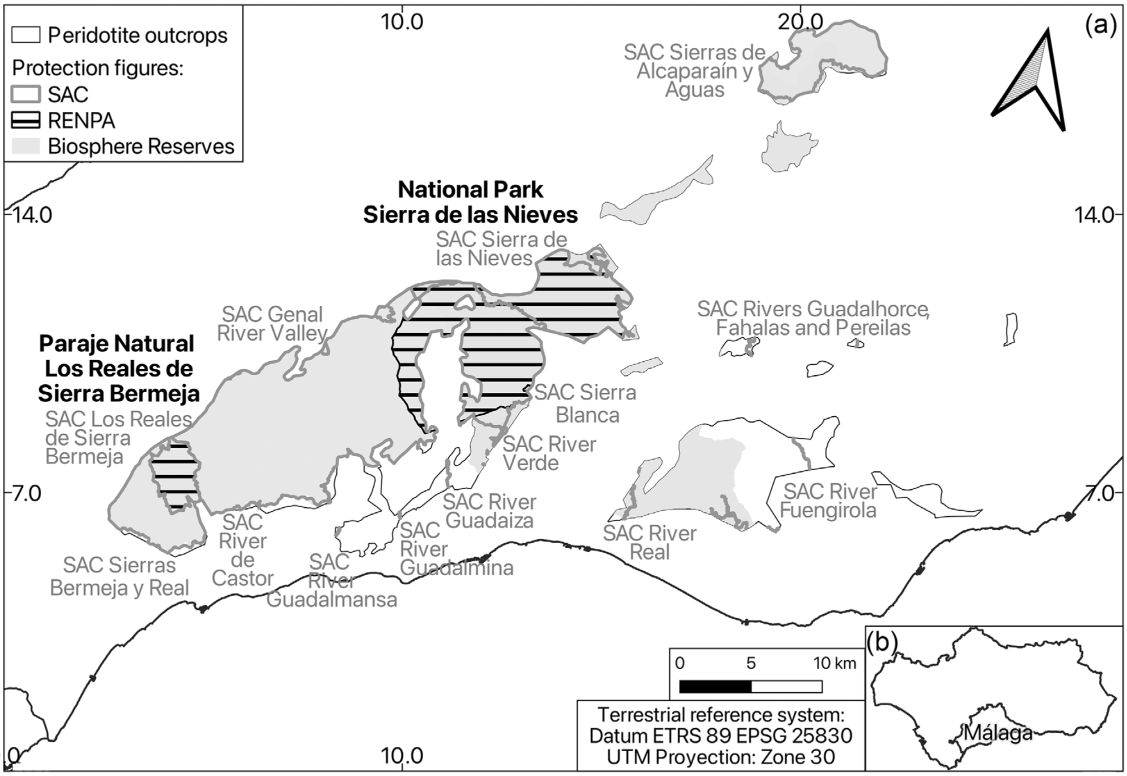

FIGURE 12 (a) Geographical distribution of the ultramafic outcrops and the areas protected under Andalusian (i.e., RENPA and DERA), Spanish (i.e., MITECO, 2023), or European law (i.e., Council Directive 92/43 CEE) or as Biosphere Reserves (i.e., by UNESCO, 2018). SAC: Special Area of Conservation, RENPA: Network of Protected Natural Areas of Andalusia (b) Location of Málaga in Andalusia province. *Source*: Data for the general cartography taken from DERA (2021).

Cabezudo (2013); Pérez-Latorre et al. (2018) or in the newly added category of regional serpentinophytes. The novel information obtained thanks to new fieldwork, new taxonomical descriptions, and the extensive use of the GBIF (2023) has permitted updating the checklist, with *Arenaria montana* subsp. *montana* var. *glandulosa* (Casimiro-Soriguer, 2020) and *Daucus setifolius* as new additions never mentioned in the previous checklists as serpentinophytes, which led us to create a new category of serpentinophytes. The nucleus of the populations of *A. montana* subsp. *montana* var. *glandulosa* (cf. Casimiro-Soriguer, 2020) present in the Iberian Peninsula lies in the serpentine mountain of Sierra Bermeja, while *D. setifolius*, at least on the Iberian Peninsula, inhabits only the southern Iberian ultramafic ecosystems (Martínez-Flores et al., 2019).

The introduction of *Genista hirsuta* subsp. *lanuginosa* in the obligate category is justified by the taxonomical and chorological changes proposed by Hidalgo-Triana and Pérez-Latorre (2019) and Devesa (2023), such that the populations of subsp. *lanuginosa* inhabiting non-serpentine substrates named at the variety level with the name of *G. hirsuta* subspecies *lanuginosa* var. *silicicola* Hidalgo-Triana & Pérez-Latorre are now identified at the subspecies level with the name of *G. hirsuta* subsp. *silicicola* (Hidalgo-Triana & Pérez-Latorre) F. Casimiro-Soriguer & Devesa. *Galium boissieranum*, *Galium viridiflorum*, *Arenaria retusa*, and *Centaurea haenseleri* have been transferred to different categories of serpentinophytes due to our new chorological treatment and data. *Galium boissieranum*, for instance, has been regarded as an obligate serpentinophyte because the populations identified under that name, in non-serpentine substrates, correspond with a new taxon named *Galium pierredmondii* Blanca, Cueto, J. Fuentes & Ortega-Oliv. (Blanca et al., 2021). Meanwhile, *Arenaria retusa* was relocated to the obligate category because the populations identified in non-peridotitic substrates correspond with *A. arundana*, as we verified when reviewing the vouchers which the identity of those populations was based upon. *Galium viridiflorum* has been classified as a sub-serpentinophyte because we found more populations in dolomites (e.g., Fuentes Carretero & Cueto Romero, 2015). Beyond that, *Centaurea haenseleri* was transferred to the preferential category based on the lasting presence of the only population inhabiting dolomites cited in Gavira and Pérez-Latorre (2005), as is also cited in Devesa (2023). Last, the relocation of *Notholaena marantae* to the new regional serpentinophyte category was made because the taxon, out of southern Iberian Peninsula, inhabits non-serpentine substrates (Salvo et al., 1990).

With respect to the taxonomical spectra, the dominance of Asteraceae among the number of serpentinophytes was detected by Pérez-Latorre, Hidalgo-Triana, and Cabezudo (2013), continued by Pérez-Latorre et al. (2018), and was present in our updated review as well. The lack of serpentinophytes in the Poaceae, as in Greece (Trigas & Iatrou, 2006), remains striking, although such was not the case in other outcrops, including in Italy (Selvi, 2007) and Portugal (Ramírez-Rodríguez et al., 2022). The most important genera by number of taxa (i.e., with at least two) were *Arenaria*, *Armeria*, *Centaurea* and *Silene*, all of which coincide with genera existing in other European outcrops, including ones in Portugal (Menezes de Sequeira & Pinto da Silva, 1992; Ramírez-Rodríguez et al., 2022), some in Italy (Selvi, 2007) such as *Armeria* and *Centaurea*, in Greece (i.e., *Silene* and *Centaurea*; Trigas & Iatrou, 2006), and in Turkey (i.e., *Silene*; Kurt et al., 2013; Reeves & Adigüzel, 2004). None of these taxa are common with the northern Moroccan serpentine flora (Ater et al., 2000). In other more distant but also Holarctic ultramafic areas, including in California (Kruckeberg, 1992; Safford et al., 2005), other families such as Liliaceae and Brassicaceae dominate, with only two examples of the latter family in Andalusia (i.e., *Alyssum serpyllifolium* and *Iberis fontqueri*). By contrast, the serpentine endemic composition of Sri Lanka, allocated in the Paleotropical kingdom, is entirely different (Rajakaruna & Bohm, 2002) due to not sharing genera with our study area, which, as Ramírez-Rodríguez et al. (2022) demonstrated for the serpentine Portuguese areas, is probably due to the distant biogeographical placement of Sri Lanka.

From a biological and ecological perspective, the perennial forms dominate over annual ones because the biological spectrum is clearly dominated by hemicryptophyte and chamaephyte biotypes, as in the world's other ultramafic ecosystems, including in Tuscany, Italy (Selvi, 2007), Portugal (Ramírez-Rodríguez et al., 2022), and Morocco (El Ghalabzouri et al., 2023). The nonexistence of phanerophytes coincides with what Selvi (2007) found in northern Italy and Pérez-Latorre, Hidalgo-Triana, and Cabezudo (2013) found previously in southern Iberia.

From a bioclimatic perspective, most of the serpentinophytes were found within at least two bioclimatic belts, which could indicate an adaptation more directed to the ultramafic substrate and its hostile characteristics and to the Mediterranean's macro bioclimate (Hidalgo-Triana & Pérez-Latorre, 2018) than an adaptation restricted to certain altitudinal belts and temperature ranges. However, there is a group of thermophilic taxa, including *Allium rouyi*, *Galatella malacitana*, and *Notholaena marantae*, that could combine their serpentine adaptation with a thermophilic adaptation. Conversely, other cases are likely driven by exceptionally scarce populations, as seen in the examples of *Euphorbia flavicoma* subsp. *bermejense* and *Peucedanum officinale* subsp. *brachyradium*. Furthermore, *Armeria colorata*, among the serpentinophytes, stands out as the farthest above the mean altitude (i.e., 800–1400 m.a.s.l), and therefore, the most orophilic.

The percentage of obligate threatened serpentinophytes according to the ARD (Cabezudo et al., 2005) was 60% (i.e., 17 taxa of 28), of which 11 taxa were included in the two high-risk categories (i.e., CR and EN) and five classifieds as VU. Surprisingly, only some of those latter obligate serpentinophytes have been included in Andalusian law, namely in the VU and RPE category. In the case of the VU category, only the obligate serpentinophytes *Armeria villosa* subsp. *serpentinicola*, *Centaurea lainzii*, and *Silene fernandezii* have been protected, while the obligates *Allium rouyi*, *Armeria colorata*, and the sub-serpentinophyte *Galium viridiflorum* have been protected by the minor designation of RPE. Species protected with the RPE designation are species included on a regional list but have a protection category less than the catalogue of protected species. It is important to highlight that none of the serpentinophytes have been protected in the highest protection category (i.e., EN). Although a high percentage of serpentinophytes are catalogued as threatened in the corresponding Andalusian red lists of vascular flora (65%), that status is not reflected in the law and even less reflected with the most threatened categories such as EN and CR, which seems to contradict the rationality, adaptive features, strict habitats, and concrete origins of serpentinophytes and their endemicity. As Millar and Libby (1991) highlighted more than 30 years ago, it is important to preserve those populations because they might represent genetically different ecotypes that involve greater degrees of genetic diversity and evolutionary fitness at the species level.

Although no work has been performed exclusively to search for new nickel hyperaccumulators in our study area, no new hyperaccumulators were discovered that Pérez-Latorre, Hidalgo-Triana, and Cabezudo (2013) had not already reported, because *Alyssum serpyllifolium* and *Saxifraga gemmulosa* are the only known hyperaccumulators on the southern Iberian Peninsula.

It is scientifically desirable and necessary to establish a checklist of serpentinophytes that encompasses all outcrops on the Iberian Peninsula (i.e., Andalusia, Galicia and Portugal), considered to be a biogeographically homogeneous framework independent of the nearest biogeographic frameworks, including North Africa, which is separated by the marine biogeographic barrier (i.e., Alboran Sea), or the rest of Europe, which is separated by orographic biogeographic barriers (i.e., the Pyrenees).

4.2 | Distribution of categories of serpentinophytes in relation to petrographic entities

To our knowledge, our study has marked the first attempt to describe the occupancy in variation of southern Iberian serpentinophytes and their categories of affinity to the various types of ultramafic substrates on which they can develop (Kurt et al., 2013; Selvi, 2007). Therefore, our study has advanced current understandings of the ecology of those very particular plants, which in some cases are capable of living only in the harsh conditions of ultramafic rocks or, in others, of being able to develop on both those hostile substrates with greater or lesser affinity depending on the composition of the type of ultramafic rock and on non-ultramafic rock substrates.

Our results suggest a pattern of possible association between the categories of serpentinophytes and the different petrographic entities of harzburgite–lherzolite and harzburgite–pyroxenite–dunite, a presence that coincides with the fact that those petrographic entities have the relatively high surface land areas in our study area (i.e., 180.52 and 91.17 km^2, respectively). That trend between the categories of serpentinophytes and the area of the different petrographic entities did not follow the area in the case of the rest of petrographic entities, because the following petrographic entities preferred by serpentinophytes were not the most abundant in terms of area. The obligate, preferential, and regional serpentinophytes showed a preference for harzburgite–lherzolite, except the sub-serpentinophytes, which preferred the harzburgite–pyroxenite–dunite.

Those results suggest that a higher occupancy could relate to the presence of certain ultramafic petrographic entities (e.g., harzburgite–lherzolite and harzburgite–pyroxenite–dunite), their mineralogical-chemical composition including heavy metals, and to the surface area of those outcrops as indicated Pérez-Latorre, Hidalgo-Triana, and Cabezudo (2013). We suggest supplementing our study with biogeochemical research to understand whether any chemical components can explain the current distribution of the serpentinophytes in our area and in the rest of the world. In other work, Manteca-Bautista et al. (2022) detected important differences in bioaccumulation factors for some of those petrographic entities in relation to the presence of nickel, and, for that reason, it could be valuable to study those geological and ecological aspects across all ultramafic ecosystems over the world.

4.3 | Distribution of serpentinophyte species in different petrographic entities

Most of the widely distributed obligate serpentinophytes have shown relatively high occupancy in different petrographic entities. However, we also found that serpentinophytes with occupancy that have not varied according to petrographic entities are geographically restricted serpentinophytes such as *Armeria colorata*, *Euphorbia flavicoma* subsp. *bermejense*, and *Peucedanum officinale* subsp. *brachyradium*, which are restricted to the Bermeja outcrop and have reduced populations (Cabezudo et al., 2005; Hidalgo-Triana & Pérez-Latorre, 2019; Pérez-Latorre et al., 2018). Such light distribution may explain why we detected no trend. The same was the case for the restricted endemism *Armeria villosa* subsp. *serpentinicola*.

Based on our study, it is impossible to explain the lack of variation in occupancy for several taxa, possibly because they are distributed across different petrographic entities. *Centaurea haenseleri*, *Notholaena marantae*, and *Daucus setifolius*, for instance, are preferential or regional serpentinophytes, and thus more flexibility in soil adaptations is expected from those species because they can live out of ultramafic rocks. The explanation for *Cephalaria boetica* and *Galium boissieranum* remains uncertain, however. The case of *Galium viridiflorum*'s tendency of positive occupancy is remarkable because the species is the only that develops in permanent streams and wet soils, which may affect the chemistry of the soils. A possible explanation is the scale of the existent geological map of the petrographic entities: some populations of studied taxa in fact inhabit different petrographic entities because the scale of our geological map is too large to capture it. It will thus be necessary for future studies to adopt a more granular scale of physico-chemical soil characteristics where the populations of each taxa live.

The number of species records and their degree of richness were higher in the outcrops and petrographic entities with larger surface areas, possibly due to their greater representation in the ecosystems studied. That finding aligns with the results of a similar study on serpentinophytes in Italy (Selvi, 2007). However, because we used GBIF herbarium data, it is essential to recognize that the number of records could have been influenced by sampling biases in herbarium collections, because those data are not always systematically or spatially collected during fieldwork and often include specimens from accessible or frequently visited areas. As a result, certain plant species or petrographic entities may be overrepresented, whereas others are underrepresented or absent in the data (Meyer et al., 2016; Szabo et al., 2023). Nevertheless, those data are a valuable resource, and, despite their limitations, they should be used cautiously. They provide valuable insights that enable progress as a crucial tool to guide actions for the conservation of biodiversity in those natural spaces.

4.4 | Richness of serpentinophytes and records per outcrop and environmental protection

The greatest richness of serpentinophytes was found in the main outcrop of Bermeja ($n = 26$), followed by the Alpujata outcrop ($n = 18$), the Aguas outcrop ($n = 15$), and the Guadalhorce Valley outcrop ($n = 2$). Our results coincide with Selvi (2007) and Pérez-Latorre, Hidalgo-Triana, and Cabezudo (2013), although the richness of Aguas resembled that of Alpujata, despite the notable difference in areas. The high richness of Aguas can be explained by the insular and bioclimatic characteristics of the outcrop; it is the northernmost outcrop of all outcrops that we studied, which may have led to a more pronounced genetic isolation than the others (MacArthur & Wilson, 2001; Selvi, 2007), while its bioclimate is more continentalized and dry (Pérez-Latorre et al., 2019). The low number of serpentinophytes and log-corrected richness in the Guadalhorce Valley may indicate that some of them have not yet been found there.

However, though the outcrop of Bermeja was the most diverse in terms of categories of serpentinophyte affinity, including obligate, preferential, regional, and sub-serpentinophyte species, and had the highest number of strictly endemic serpentinophyte species, it is important to note that the Alpujata and Aguas outcrops exhibited similar corrected richness to Bermeja with notably inferior areas and with the presence of restricted endemic serpentinophytes, as is the case of the Aguas outcrop. Despite that ecological significance, it remains evident that there is an urgent need for the comprehensive protection of those ultramafic outcrops.

Due to the exclusive presence of serpentinophyte flora, the southern Iberian outcrops should all be subject to some form of protection as natural spaces, including as phylogeographic refuges and hotspots (Bañares Baudet, 2003; Médail & Diadema, 2009). However, it is important to note that the Alpujata outcrop lacks any form of protection, including by European law (i.e., Council Directive 92/43/EEC, 1992). Furthermore, the most significant outcrop in all of Western Europe, Bermeja, has the necessary conditions to be a national park under Spanish law, though such has not yet been realized.

Although a portion of Bermeja's surface area enjoys protection through RENPA's designations, there is an urgent need to establish comprehensive protection for the entire Sierra Bermeja region, as well as the other outcrops that currently lack any form of designation affording environmental protection (i.e., Aguas, Alpujata, and Guadalhorce Valley). Other countries have already recognized the significance of such rock formations (e.g., ophiolites and peridotites), as exemplified by Canada's Gros Morne National Park's UNESCO World Heritage Site status (UNESCO, 2023) and the Shebenik-Jabllanicë National Park in Albania, which is characterized by one of the most important outcrops of the Mirdita ophiolitic formation (Fanelli et al., 2018).

The call for comprehensive protection for Sierra Bermeja, the largest Western-Mediterranean ultramafic outcrop, echoes the measures taken in various parts of the world, where unique geological ultramafic formations and the ecosystems that they support are safeguarded within national parks or other protection figures (Fanelli et al., 2018; Kruckeberg, 2004). Sierra Bermeja's ecological and environmental value make it an ideal candidate for such protection (Gómez-Zotano et al., 2015). To ensure the long-term preservation of its biodiversity, landscapes, geomorphology, and cultural heritage, designating Sierra Bermeja as a national park in its entirety is a measure that not only aligns with international best practices but is also an imperative step toward securing the legacy of such a remarkable area.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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