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Contribution to the knowledge of Portuguese serpentine flora: ecological characteristics, endemic plants, and implications for biodiversity conservation

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ABSTRACT

Serpentine areas are scarce in the world, but contain a large number of endemic taxa. These areas have, in many cases, been little or not at all surveyed from a vegetation and biodiversity conservation point of view. The most important Portuguese serpentine outcrops are found in northeastern Portugal, particularly in the Bragança-Vinhais and Morais massifs. Here, we present a complete ecological-floristic check-list of serpentinophites that are found in these areas since this knowledge is essential for their evaluation, management and conservation. A total of 25 taxa, classified into three categories with different grades of serpentinophily, were included in the list: (1) obligate serpentinophytes (exclusively on serpentine), (2) endemic or widespread taxa that in Portugal occur exclusively in ultramafic outcrops, and (3) preferential serpentinophytes (most of the distribution range, at least 90% of populations, are found on serpentine). Genera common to other Iberian serpentine areas (Andalusian serpentine flora) are *Odontarrhena*, *Arenaria*, *Armeria*, *Asplenium*, *Paragymnopteris*, *Saxifraga* and *Silene*. The majority of the studied serpentinophytes (72%) occurred in endemic and highly specialized plant communities. About half of the studied serpentinophytes (48%) are assigned in some IUCN threat category. Consequently, it is necessary to implement conservation measures to guarantee the protection of these habitats.

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Introduction

Peridotites outcrops constitute unique type of rocks on Earth due to both plutonic igneous origin and chemical composition (Brooks 1987). Peridotites, through the process of hydration, converted into serpentines. These, also called ultramafic rocks, are soils developed from different types of ophiolithic bedrock, with pH values varying from basic to ultrabasic (pH 6.5–8). These soils are characterized by having low concentrations of principal plant nutrients (N, P, K, Ca). In contrast, they have high levels of Mg and Fe, toxic trace elements as Cr, Ni and Co and a high Mg/Ca ratio (Brooks 1987; Proctor and Nagy 1992).

The presence of these cytotoxic elements, together with other physical properties, exerts a high selective pressure on the flora and a negative effect upon the growth of plants. Serpentine areas are mainly characterized by low plant production, low diversity, high number of endemic species and distinct floristic composition in comparison with the vegetation of adjacent regions (Whittaker 1954). As a consequence, only a relatively low percentage of species, named serpentinophytes or serpentinophilous, are adapted to grow on serpentines. These species have developed typical morpho-functional and physiological adaptations (serpentine-morph syndrome) such as stenophylly, glaucous and glabrous leaves, enlarged root systems, plagiotropism, and nanism (Pichi-Sermolli 1948; Kruckeberg 1984). Kruckeberg (2002) classified the serpentinophytes into three categories: 1) those species that grow exclusively on serpentines (obligate serpentinophytes or endemic taxa), 2) those species whose distribution is mainly associated with serpentines, but they can occasionally grow on other substrates (preferential serpentinophytes), and 3) those species inhabiting a wide variety of substrates, including serpentines (bodenvag taxa).

The surface occupied by the serpentines does not exceed 1% of the earth´s surface. They are scarce, fragmented and highly variable in extent and distance with a broad spectrum of isolation degree. They occur in extensive regional areas or, more often, as local outcrops, making up a particular system of ecological islands (geologic island or edaphic island) (Harrison and Inouye 2002). Due to their rarity, scarcity and unique ecological characteristics, they are considered as important centres of floristic differentiation and speciation, phylogeographic refugia and areas for plant conservation (Kruckeberg 1986, 2002; Chiarucci et al. 1998; Palmer and Smart 2001; Sequeira et al. 2010).

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In Europe, the Balkans is the most important area for obligate serpentinophytes (Brooks 1987; Stevanović et al. 2003). In the western Mediterranean Basin, Italy presents lesser extent of serpentines that Balkans but it also harbours a great diversity of serpentinophytes (Vergnano Gambi 1992), especially in the Tuscany region (Chiarucci and De Dominicis 2001). In the Iberian Peninsula, the most important and extensive areas of serpentines are located in the southern Iberian Peninsula (Andalusia), covering a total area of 430 km^2 (e.g., Pérez-Latorre et al. 2013). The westernmost serpentine areas, within the western Mediterranean Basin, are found in northwestern Spain (Melide, Galicia) and northeastern Portugal (Trás-os-Montes).

The flora and vegetation of Portuguese serpentine areas was firstly studied by W. Rothmaler and A.R. Pinto Silva when they visited the region in June of 1939 (Aguiar 2001). Since then several authors have surveyed the region (Mendonça and Vasconcellos 1944–1962; Pinto da Silva 1970; Sequeira and Pinto da Silva 1992; Aguiar et al. 1998, 2013; Aguiar 2001). Likewise, other authors have reported the presence of hyper-acumulators of Ni in the serpentine Portuguese flora (Sequeira 1969; De la Fuente et al. 2007). All of them stressed the scientific importance of the ultramafic outcrops of northeastern Portugal. Consequently, Portuguese serpentine flora deserves further attention from several points of view, including taxonomic, ecological, phytogeographic and conservation approaches.

In this study, we aim to (1) elaborate an ecological-floristic checklist of serpentinophytes that occur in northeastern Portugal, (2) provide taxonomic, chorological, ecological, syntaxonomic and conservation data for each serpentine taxon, and (3) compare Portuguese serpentine flora with other Mediterranean serpentine flora, as for example Italian serpentine flora and the Iberian serpentine flora of Melide (Galicia, northwestern Iberian Peninsula) and Andalusia (southern Iberian Peninsula).

Material and methods

Study area

The study area is located in south-western Europe (Iberian Peninsula), namely in northeastern Portugal (41° **25**′ N, 41° **54**′ W) (Figure 1). The mean annual temperature is 12.4**°C** and mean annual precipitation is 720 mm (Sequeira et al. 2010). The study area is biogeographically included in the Lusitan-Duriensean biogeographical sector (Carpetan Leonese subprovince, Mediterranean West Iberia province). A unique climax forest developed in northeastern Portugal consists of thermophilous forests of *Quercus rotundifolia* Lam., with *Q. suber* L. and *Q. faginea* Lam., corresponding to the association *Genisto hystricis-Quercetum rotundifoliae* (Aguiar et al. 2013).

The study area has important serpentine outcrops which occur in two large massifs, with an extremely complex petrology (Aguiar 2001), and occupying a total area of 80 km^2 (Figure 1): 33 km^2 (41%) corresponds to the Bragança-Vinhais massif towards the north, and 47 km^2 (59%) to the Morais massif towards the south (Pinto da Silva 1970). The Bragança-Vinhais massif is found between 600 and 1060 m a.s.l., with a mean annual temperature of 12.8 °C and a mean annual precipitation of 619 mm. It is included in the supra-mediterranean bioclimatic belt. In the case of the Morais

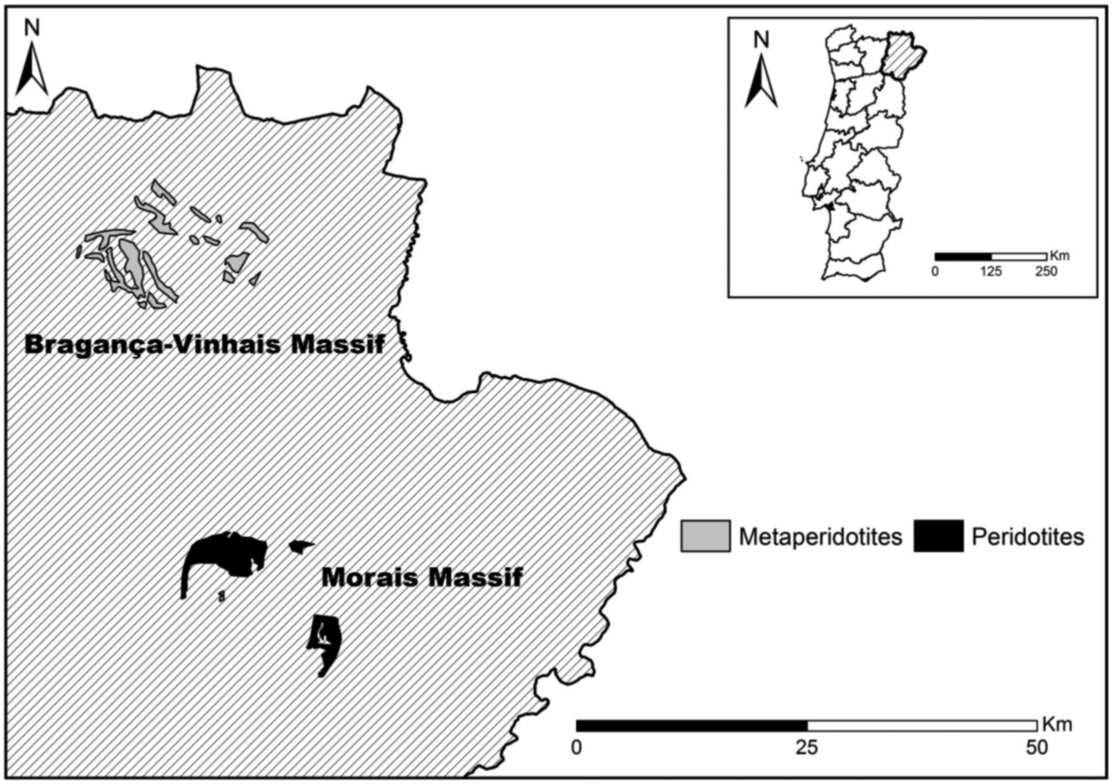

Figure 1. Study area in northeastern Portugal. Location of the peridotites and metaperidotites (ultramafic outcrops) in the Bragança-Vinhais and Morais massifs.

massif, the altitudinal range varies between 300 and 900 m a.s.l., with a mean annual temperature of 14.6 °C and a mean annual precipitation of 506 mm. It is mainly included in the mesomedierranean bioclimatic belt (Monteiro-Henriques and Aguiar 2011). The Bragança-Morais complex is related to the Cabo Ortegal ones in Galicia (NW Spain). The peculiarities of the latter are described by Pereira et al. (2008) and references therein.

Taxonomical and syntaxonomical nomenclature

The nomenclature used for taxa cited in the text was that of Euro + Med PlantBase project (https://www.emplantbase.org); the exceptions, together with synonyms of each taxon cited, are indicated in the floristic appendix (Appendix 1).

The syntaxonomy of the plant communities mentioned and studied follow the criteria of Rivas-Martínez (2011) and Costa et al. (2012) (see Appendix 2).

Data collection

We prepared a list of species that could be considered as serpentinophytes by consulting several sources. Firstly, we conducted an exhaustive bibliographical search to select those species cited as possible serpentinophytes (e.g., García 1942, 1944; Mendonça and Vasconcellos 1944–1962; Pinto da Silva 1970; Sequeira and Pinto da Silva 1992; Aguiar et al. 1998, 2013; Aguiar 2001). Then, we completed the information with chorological and ecological data obtained from Amich et al. (2004) and several databases (the global biodiversity information facility (GBIF) and Flora-On). The conservation data (IUCN threat category) were obtained from Aguiar 2001, Aguiar et al. (2013) and Carapeto et al. (2020). Likewise, we performed several surveys in the outcrops of Bragança-Vinhais and Morais massifs since 2005 to obtain several data, such as plant collecting, phenology, phytosociology (vegetation relevés), number and distribution of populations, habitat and altitude. Bioclimatic belt and ombrotype were obtained from Rivas-Martínez et al. (2011). The collected specimens were deposited in different herbaria (abbreviations are in accordance with Index Herbariorum; Thiers 2010 (continuously updated): BRESA, HVR and SALA.

We classified the study taxa, following the criteria established by Kruckeberg (2002) with minor modifications, into three categories: (1) obligate serpentinophytes (exclusively on serpentine), (2) endemic or widespread taxa that in Portugal occur exclusively in ultramafic outcrops, and (3) preferential serpentinophytes (most of the distribution range (at least 90% of populations) is found on serpentine). The category “obligate serpentinophytes” was divided into four subcategories, depending on the endemicity of serpentinophytes: (1) obligate serpentinophytes of Iberian ultramafic rocks, (2) exclusive obligate serpentinophytes in the Bragança and Morais massifs, (3) exclusive obligate serpentinophytes in the Bragança massif, and (4) exclusive obligate serpentinophytes in the Morais massif. The following data were provided for each taxon: life-form, habitat, bioclimatic belt, altitude range, ombrotype, phytosociology, distribution, flowering (or sporulation) season and IUCN threat categories.

Results

Obligate serpentinophytes

Exclusive obligate serpentinophytes in the Bragança-Vinhais and Morais massifs

Antirrhinum rothmaleri (P.Silva) Amich, Bernardos & García-Barriuso

Hemicryptophyte. Meso-supramediterranean (525–750 m). Subhumid-humid. Lithosols, stony areas and rock fissures. Secondary perennial communities, dwarf-chamaephytes grassland-like on lithosols, in the endemic association *Armerietum eriophyllae* (*Armerion eriophyllae*). Endemism of the Bragança-Vinhais and Morais massifs (Trás-os-Montes (hereafter TM)). V-VI. EN (Aguiar 2001; Carapeto et al. 2020); CR (García-Barriuso et al. 2012; Aguiar et al. 2013).

Arenaria querioides* subsp. *fontiqueri (P.Silva) Rocha Afonso

Chamaephyte. Meso-supramediterranean (525–850 m). Subhumid-humid. Lithosols, stony slopes and cleared scrublands. Secondary perennials communities, dwarf-chamaephytes grassland-like on lithosols, in the endemic associations *Arenario fontiqueri-Armerietum marizii* and *Armerietum eriophyllae* (*Armerion eriophyllae*) (Aguiar et al. 1998, 2013). Endemism of the Bragança-Vinhais and Morais massifs (TM). V-VI. LR(LC) (Aguiar 2001; Carapeto et al. 2020); LR(NT) (Aguiar et al. 2013).

Dianthus laricifolius* subsp. *marizii (Samp.) Franco

Chamaephyte. Meso-supramediterranean (500–1000 m). Subhumid-humid. Rock fissures, stony slopes, perennial meadows in cleared scrublands on lithosols. Secondary perennial communities, dwarf-chamaephytes grassland-like on lithosols, in the endemic association *Armerietum eriophyllae* (*Armerion eriophyllae*). Endemism of the Bragança-Vinhais and Morais massifs (TM). V-IX. LR(LC) (Aguiar 2001; Aguiar et al. 2013; Carapeto et al. 2020). The subspecies is also included in Annexes II and IV of the EU Habitat Directive 92/43.

Helictochloa lusitanica (Romero Zarco) Romero Zarco

Hemicryptophyte. Meso-supramediterranean (400–900 m). Subhumid-humid. Rock fissures, stony habitats and leptosols. Pioneer tall perennial grasslands, in the endemic association *Seseli peixotoani-Avenuletum lusitanicae* (*Potentillo montanae-Brachypodion rupestris*). Endemism of the Bragança-Vinhais and Morais massifs (TM). IV-VI. VU (Aguiar 2001; Aguiar et al. 2013; Romero Zarco 2018; Carapeto et al. 2020).

Exclusive obligate serpentinophytes in the Bragança-Vinhais massif

Armeria eriophylla Willk.

Chamaephyte with rosettes. Supramediterranean (700–900 m). Humid. Dry perennial grasslands, rock fissures and lithosols. Secondary perennial communities, dwarf-chamaephytes grassland-like on lithosols, in the endemic association *Armerietum eriophyllae* (*Armerion *eriophyllae*). Endemism of the Bragança-Vinhais massif (TM). V-VI. LR(LC) (Aguiar 2001), LR(NT) (Aguiar et al. 2013; Carapeto et al. 2020).

Festuca brigantina (Markgr.-Dann) Markgr.-Dann.

Hemycryptophyte. Supramediterranean (700–1000 m). Humid. Lithosols and regosols, stony areas and rock fissures. Secondary perennial communities, dwarf-chamaephytes grassland-like on lithosols and regosols, in the endemic association *Armerietum eriophyllae* (*Armerion eriophyllae*). Endemism of the Bragança massif (TM). VI-VI. VU (Aguiar 2001, Carapeto et al. 2020); EN (Aguiar et al. 2013). Regarding the Mediterranean basin as scope of the conservation assessment, its conservation status is CR (Critically endangered) (Caldas et al. 2017). The subspecies is also included in the Annexes II and IV of the EU Habitat Directive 92/43.

Exclusive obligate serpentinophytes in the Morais massif

Armeria langei* subsp. *marizii (Daveau) C.Aguiar, Sánchez-Mata & Monteiro-Henriques

Chamaephyte with rosettes. Meso-supramediterranean (500–800 m). Subhumid-humid. Dry perennial grasslands, rock fissures and lithosols. Secondary perennial communities, dwarf-chamaephytes grassland-like on lithosols, in the endemic association *Arenario fontiqueri-Armerietum marizii* (*Armerion eriophyllae*). Endemism of the Morais massif (TM). V-VII. LR(NT) (Aguiar et al. 2013; Carapeto et al. 2020).

Obligate serpentinophyte endemic of Iberian ultramafic rocks

Asplenium adiantum-nigrum* subsp. *corunnense (H.Christ) Rivas-Mart.

Hemicryptophyte. Meso-supramediterranean (550–1000 m). Humid. Shaded and wet rock fissures. Umbrophilic rupicolous vegetation, in the endemic association *Umbilico violacei-Asplenietum corunnensis* (*Phagnalo saxatilis-Cheilanthion maderensis*). Endemism of the Iberian Peninsula. In Portugal the species occurs exclusively in TM, both in the Bragança-Vinhais and Morais massifs. V-XII. VU (Aguiar 2001); LR(NT) (Aguiar et al. 2013).

Iberian endemism or widespread taxa that in Portugal occur exclusively in ultramafic outcrops

Odontarrhena serpyllifolia (Desf.) Jord. & Fourr.

Chamaephyte. Meso-supramediterranean (350–850 m). Subhumid-humid. Fallow lands, roadsides, and *Cistus* shrublands. Subnitrophiluous chamaephytes communities, in the endemic association *Alysso lusitanici-Santolinetum semidentatae* (*Artemisio glutinosae-Santolinion rosmarinifoliae*). South Europe and north Africa. Almost the whole Iberian Peninsula; in Portugal exclusively in TM. IV-VII. LR(LC) (Aguiar 2001; Aguiar et al. 2013; Carapeto et al. 2020). The subspecies is also included in Annex V of the EU Habitat Directive 92/43.

Anthyllis vulneraria* subsp. *sampaioana (Rothm.) Vasc.

Hemicryptophyte. Supramediterranean (700–900 m). Humid. Lithosols, stony areas and meso-xerophile grasslands. Terophytic communities developed on rich soils belonging to the alliance *Brachypodion distachyi*. Western Alps and north Iberian Peninsula; in Portugal the species occurs in TM and BA (Beira Alta). IV-VII. LR(NT) (Aguiar 2001); VU (Aguiar et al. 2013); LR(LC) (Carapeto et al. 2020).

Astragalus incanus* subsp. *nummularioides (Desf.) Maire

Hemicryptophyte. Supramediterranean (500–900 m). Humid. Lithosols and stony areas. Secondary perennial communities, dwarf-chamaephytes grassland-like on lithosols, in the endemic association *Armerietum eriophyllae* (*Armerion eriophyllae*). Iberian Peninsula and northwest Africa; in Portugal exclusively in TM. III-VI. VU (Aguiar 2001; Aguiar et al. 2013); EN (Carapeto et al. 2020).

Bromus squarrosus L.

Therophyte. Supramediterranean (500–925 m). Humid. Slopes, stony places and roadsides. Semi-nitrophilous annual vernal communities of *Thero-Brometalia*. North Africa, Europe, western Russia and Middle East; in Portugal exclusively in TM. IV-VI. VU (Aguiar 2001; Carapeto et al. 2020), EN (Aguiar et al. 2013).

***Elytrigia intermedia* subsp. *trichophora* (Link) Á.Löve & D.Löve**

Hemicryptophyte. Supramediterranean (500–925 m). Humid. Perennial grasslands. Semi-nitrophilous annual vernal communities of *Thero-Brometalia*. Europe; in Portugal exclusively in TM. V-VI. DD (Aguiar 2001; Aguiar et al. 2013); CR (Carapeto et al. 2020). Although the subspecies has not been found again in recent years, its current presence cannot yet be ruled out (see Carapeto et al. 2020).

Gagea pratensis (Pers.) Dumort.

Geophyte. Supramediterranean (500–925 m). Humid. Rock fissures, slopes, stony places, humid grasslands and scrublands. Secondary perennial communities, dwarf-chamaephytes grassland-like on lithosols, in the endemic association *Armerietum eriophyllae* (*Armerion eriophyllae*) and in the class *Festuco-Brometea*. Europe and northwest Africa; It is distributed by the northern half of the Iberian Peninsula; in Portugal exclusively in TM. III-IV. EN (Aguiar 2001; Aguiar et al. 2013); VU (Carapeto et al. 2020).

Jasonia tuberosa (L.) DC.

Hemicryptophyte. Supramediterranean (500–950 m). Humid. Rock fissures and commonly flooded slopes, stony places and roadsides. Communities in seasonally flooded areas (*Deschampsion mediae*; *Holoschoenetalia*). Southwest Europe (Spain, Portugal and S France); in Portugal exclusively in TM. VI-VIII. VU (Aguiar 2001); EN (Aguiar et al. 2013); LR(NT) (Carapeto et al. 2020).

Paragymnopteris marantae (L.) K.H.Shing

Hemicryptophyte. Meso-supramediterranean (300–900 m). Subhumid-humid. Rock fissures in sunny and stony slopes. Rupicolous and heliophytic vegetation in serpentinites, in the endemic association *Notholaenetum marantae* (*Phagnalo saxatilis-Cheilanthion maderensis*) (García-Barriuso et al. 2011b). Mediterranean, Pontic-Mediterranean, Ethiopia, Yemen and Himalaya. Above all in the east and south of the Iberian Peninsula, rare in the northwest (Pontevedra (PO, Spain); in Portugal exclusively in TM. I-VII. VU (Aguiar 2001; García-Barriuso et al. 2011b; Aguiar et al. 2013); LR(NT) (Carapeto et al. 2020).

Reseda virgata Boiss. & Reut.

Chamaephyte. Meso-supramediterranean (400–900 m). Subhumid-humid. Lithosols, slopes and roadsides. Secondary perennial communities, dwarf-chamaephytes grassland-like on lithosols, in the endemic association *Armerietum eriophyllae* (*Armerion eriophyllae*). Endemism of the northern subplateau of the Iberian Peninsula; in Portugal, the species occurs in TM and Alentejo (Castro Antunes et al. 2019). IV-VII. LR(NT) (Aguiar 2001); LR(LC) (Aguiar et al. 2013).

Saxifraga dichotoma Willd.

Hemicryptophyte. Supramediterranean (600–900 m). Humid. Lithosols, stony areas and *Quercus rotundifolia* clearings. Secondary perennial communities, dwarf-chamaephytes grassland-like on lithosols, in the endemic association *Armerietum eriophyllae* (*Armerion eriophyllae*). Western Mediterranean Basin; in Portugal exclusively in TM. II-V. EN (Aguiar 2001; Aguiar et al. 2013); VU (Carapeto et al. 2020).

Silene legionensis Lag.

Hemicryptophyte. Supramediterranean (500–925 m). Humid. Dry perennial grasslands, rock fissures and stony places. Pioneer tall perennial grasslands, in the endemic association *Seseli peixotoani-Avenuletum lusitanicae* (*Potentillo montanae-Brachypodion rupestris*). Iberian endemism, except for a large part of north, east, southwest and centrewest; in Portugal exclusively in TM. VI-VII. VU (Aguiar 2001; Aguiar et al. 2013; Carapeto et al. 2020).

Ventenata dubia (Leers) Coss.

Therophyte. Supramediterranean (500–925 m). Humid. Dried up wetlands and open areas. South Europe, Middle East and north Africa; in Portugal exclusively in TM. V-VI. DD (Aguiar et al. 2013); EN (Carapeto et al. 2020). The species was rediscovered 75 years later (2017) after it was first cited by García (1942).

Xeranthemum cylindraceum Sm.

Therophyte. Supramediterranean (500–900 m). Humid. Fallow lands, grasslands and cleared scrubland. Therophytic communities developed on rich soils belonging to the order *Brachypodion distachyi*. South Europe, southwest Asia and northwest Africa; in Portugal exclusively in TM. VI-VI. VU (Carapeto et al. 2020).

Xeranthemum inapertum (L.) Mill.

Therophyte. Supramediterranean (500–800 m). Humid. Scrubland clearings, stony slopes and rock fissures in sunny rocky areas. Therophytic communities developed on rich soils belonging to the order *Brachypodion distachyi*. Mediterranean region, southwest and centre Europe and southwest Asia; in Portugal exclusively in TM. V-VI. VU (Carapeto et al. 2020).

Preferential serpentinophytes

Armeria langei* subsp. *daveaui (Cout.) P.Silva

Chamaephyte with rosettes. Meso-supramediterranean (500–950 m). Subhumid-humid. Mesotrophic perennial grasslands, cleared shrubs, *Quercus pyrenaica* clearings and rock fissures. Mesotrophic perennial grasslands, in the endemic association *Armerio daveaui-Agrostietum castellanae* (*Agrostion castellanae*). Endemism of northwestern Iberian Peninsula; in Portugal exclusively in TM. V-VII. LR(NT) (Aguiar 2001; Aguiar et al. 2013; Carapeto et al. 2020).

Santolina semidentata Hoffmanns. & Link

Chamaephyte. Meso-supramediterranean (350–900 m). Subhumid-humid. Fallow lands, roadsides, and stony slopes with scrublands. Subnitrophiluous chamaephytes communities, in the endemic association *Alysso lusitanici-Santolinetum semidentatae* (*Artemisio glutinosae-Santolinion rosmarinifoliae*). Endemism of northwestern Iberian Peninsula; in Portugal exclusively in TM. V-VI. LR(LC) (Aguiar 2001; Aguiar et al. 2013; Carapeto et al. 2020). Likewise, the species is also included in Annexes II and IV of the EU Habitat Directive 92/43.

Seseli montanum* subsp. *peixotoanum (Samp.) M.Laínz

Hemicryptophyte. Meso-supramediterranean (400–900 m). Subhumid-humid. Lithosols, mesophile perennial grasslands and cleared scrubland. Pioneer tall perennial grasslands, in the endemic association *Seseli peixotoani-Avenuletum lusitanicae* (*Potentillo montanae-Brachypodion rupestris*). Endemic of the northwestern Iberian Peninsula; in Portugal exclusively in TM. VI-IX. LR(LC) (Aguiar 2001; Aguiar et al. 2013; Carapeto et al. 2020).

Discussion

The floristic composition of the Portuguese serpentine areas consists of 13 families, 22 genera and 25 taxa. A total of 22 (2 pteridophyte, 6 monocots and 14 dicots) are considered as obligate serpentinophytes in Portugal (Table 1). From these, 7 are local endemic taxa from the Bragança-Vinhais massif (2), Morais massif (1) or both (4). The Bragança-Vinhais massif is more diverse in endemic species than Morais massif due, partly, to the concentration of these endemic species at higher altitudes (Sequeira et al. 2010). From a biogeographical context, the proximity of the Cantabrian Mountain Range may have facilitated the migration of a mountain basophyllous-neutrophyllous species. One taxa, considered as obligate serpentinophyte, has a wider distribution: *Asplenium adiantum nigrum* subsp. *corunnense* (Iberian Peninsula). 14 taxa are Iberian endemics or widespread taxa which occur exclusively in serpentines in Portugal (Table 1). 3 taxa are preferential serpentinophytes, which have a restricted distribution range to the northwestern Iberian Peninsula. The endemicity rate for obligate serpentinophytes in Portugal is 36%. This value is lower than in other serpentine areas of Iberian Peninsula, such as the Ronda Mountain Range (Malaga province), particularly in Sierra Alpujata where it reaches 64% in a similar extent (71 km^2) to the study area (80 km^2) (Pérez-Latorre et al. 2013). In contrast, the endemicity rate is similar to that in the Galician areas (37%), an area that present many similarities with the study area (see Rodríguez-Oubiña and Ortiz 1991).

The study area has strong floristic affinities with other Iberian serpentine areas and shares great number of genera, e.g., Galicia (*Odontarrhena*, *Anthyllis*, *Armeria*, *Festuca*, *Santolina* and *Seseli*) (Rodríguez-Oubiña and Ortiz 1991) and the Ronda Mountain Range (*Odontarrhena*, *Arenaria*, *Armeria*, *Asplenium*, *Paragymnopteris* (≡ *Notholaena*), *Saxigrafa* and *Silene*) (Pérez-Latorre et al. 2013) as well as with other Mediterranean serpentine areas in the world, e.g., Italy (*Odontarrhena*, *Anthyllis*, *Antirrhinum*, *Asplenium*, *Armeria*, *Bromus*, *Dianthus*, *Festuca*, *Paragymnopteris* and *Silene*) (Selvi 2007), Turkey (*Odontarrhena*, *Arenaria*, *Asplenium*, *Astragalus*, *Bromus*, *Festuca*, *Paragymnopteris* and *Silene*) (Kurt et al. 2013), and

Table 1. List of serpentinophytes found in the ultramafic outcrops of the Bragança and Morais massifs (northeastern Portugal).

Family	Taxa	Taxonomic category	Serpentinophytes type
Apiaceae	*Seseli montanum* subsp. *peixotoanum*	Dicot	PS
Aspleniaceae	*Asplenium adiantum-nigrum* subsp. *corunnense*	Pteridophyta	OS I
Asteraceae	*Jasonia tuberosa*	Dicot	OS P
	Santolina semidentata	Dicot	PS
	Xeranthemum cylindraceum	Dicot	OS P
	Xeranthemum inapertum	Dicot	OS P
Brassicaceae	*Odontarrhenaserpyllifolium*	Dicot	OS P
Caryophyllaceae	*Arenaria querioides* subsp. *fontiqueri*	Dicot	OS B&M
	Dianthus laricifolius subsp. *marizii*	Dicot	OS B&M
	Silene legionensis	Dicot	OS P
Fabaceae	*Anthyllis vulneraria* subsp. *sampaioana*	Dicot	OS P
	Astragalus incanus subsp. *nummularioides*	Dicot	OS P
Liliaceae	*Gagea pratensis*	Monocot	OS P
Plumbaginaceae	*Armeria eriophylla*	Dicot	OS B
	Armeria langei subsp. *marizii*	Dicot	OS M
	Armeria langei subsp. *daveaui*	Dicot	PS
Poaceae	*Elytrigia intermedia* subsp. *trichophora*	Monocot	OS P
	Helictochloa lusitanica	Monocot	OS B&M
	Festuca brigantina	Monocot	OS B
	Ventenata dubia	Monocot	OS P
	Bromus squarrosus	Monocot	OS P
Pteridaceae	*Paragymnopteris marantae*	Pteridophyta	OS P
Resedaceae	*Reseda virgata*	Dicot	OS P
Saxifragaceae	*Saxifraga dichotoma*	Dicot	OS P
Scrophulariaceae	*Antirrhinum rothmaleri*	Dicot	OS B&M

Serpentinophyte type: OS I, Obligate serpentinophye endemic of Iberian ultramafic rocks; OS B&M, obligate serpentinophytes in the Bragança-Vinhais and Morais massifs; OS B, obligate serpentinophytes in the Bragança-Vinhais massif; OS M, obligate serpentinophytes in the Morais massif; OP, endemic and widespread taxa that in Portugal occur exclusively in ultramafic outcrops; and PS, preferential serpentinophytes.

California (*Antirrhinum*, *Arenaria*, *Astragalus*, *Bromus*, *Festuca* and *Silene*) (Safford et al. 2005). The floristic relationships are less similar with other worldwide serpentine territories: Bulgaria (*Odontarrhena*, *Festuca*, *Paragymnopteris*) (Tzonev et al. 2013); Greece (*Odontarrhena* and *Silene*) (Trigas and Iatrou 2006); the Balkans region (*Odontarrhena*, *Bromus*, *Dianthus* and *Silene*) (Stevanović et al. 2003), and Morocco (*Paragymnopteris*) (Ater et al. 2000). The serpentine vegetation of Sri Lanka is totally different (Rajakaruna and Bohm 2002), not sharing genera in common with our study area. Given the insular consideration of ophiolitic outcrops (MacArthur and Wilson 1967; Selvi 2007), the opposite relationship between the degree of endemicity (high) and floristic richness (low) is consistent with what happens largely in insular ecosystems of the Mediterranean Basin (Médail and Verlaque 1997).

Two contrasting physiological strategies have evolved in serpentine species to adapt to these soils with high concentrations of toxic metals: (1) hyperaccumlators (i.e., those with a high responsiveness of accumulating toxic metals in their leaves) and (2) excluders, i.e., those that contain low concentrations of toxic metals in their leaves. Both strategies exhibited by different species coexist in ultramafic outcrops of Portugal. Thus, examples of Ni-hypercaccumlators are *Odontarrhena serpyllifolium*, firstly reported in Portuguese serpentines by Sequeira (1969), and *Antirrhinum rothmaleri* (García-Barriuso et al. 2012) while *Paragymnopteris marantae* is a Ni excluder.

Odontarrhena serpillyfolium is considered a nickel hyper-accumulator, in other words, it has a high capacity for Ni accumulation, especially in the aerial parts, reaching higher concentrations than $5000\,mg\,kg^{-1}$dry weight (Morais et al. 2015). The interest for this Ni accumulating species is increasing in all fields, including geology, botany, agriculture and biotechnology. Such species have several applications, for example, in defining and delimiting the area occupied for a type of soil with ultramafic origin from their distribution range or in phytoremediation, phytomining and phytocorrection. The species is used for the development of transgenic hyperaccumulators, identifying the genetic mechanisms and genes involved in the uptake, translocation and sequestration of Ni.

From a structural point of view, the perennial forms dominate over annual ones. The biological spectrum is clearly dominated by hemicryptophytes (12, 48%), followed by chamaephytes (8, 32%), therophytes (4, 16%) and geophytes (1, 4%) (Table 2). These data are in line with those indicated for the serpentine flora in other sites across the Mediterranean basin, such as the southeast of the Iberian Peninsula (Pérez-Latorre et al. 2013) and Tuscany (Italy) (Selvi 2007).

Owing to the floristic singularities of these territories, the flora and vegetation of the Bragança-Vinhais and Morais massifs have been well studied (Pinto da Silva 1970; Aguiar et al. 1998, 2013; Aguiar 2001). A total of seven endemic associations have been described in these territories (Appendix 1 and Table 3). Five vegetation types, which include the seven

Table 2. Number of taxa and percentage of life-forms of the studied serpentinophytes.

Life-form types	Number of taxa	Percentage (%)
Therophyte	4	16
Geophyte	1	4
Hemicryptophyte	12	48
Chamaephyte	8	32

Table 3. Number of serpentinophytes included in each syntaxon and its habitat.

		Serpentinophytes	
Syntaxon	Vegetation type/habitat	O	P
Armerietum eriophyllae	Secondary perennial communities	8	–
Arenario fontiqueri-Armerietum marizii	Secondary perennial communities	2	–
Seseli peixotoani-Avenuletum lusitanicae	Pioneer tall perennial grasslands	2	1
Armerio daveaui-Agrostietum castellanae	Mesotrophic perennial grasslands	–	1
Umbilico violacei-Asplenietum corunnensis	Rupicolous vegetation	1	–
Notholaenetum marantae	Rupicolous vegetation	1	–
Alysso lusitanici-Santolinetum semidentatae	Subnitrophilous vegetation	1	1
Deschampsion mediae	Seasonally wet grasslands	1	–
Brachypodion distachyi	Terophytic communities	3	–
Thero-Brometalia	Semi-nitrophilous annual vernal communities	2	–

O, obligate; P, preferential.

endemic associations, occur in the ultramafic outcrops of northeastern Portugal: (1) secondary perennial communities of the *Armerietum eriophyllae* in the Bragança-Vinhais massif or of the *Arenario fontiqueri-Armerietum marizii* in the Morais massif; (2) pioneer tall perennial grasslands of the *Seseli peixotoani-Avenuletum lusitanicae*; (3) mesotrophic perennial grasslands of the *Armerio daveaui-Agrostietum castellanae*; (4) rupicolous vegetation of the *Umbilico violacei-Asplenietum corunnensis* and of the *Notholaenetum marantae*; and (5) subnitrophilous vegetation of the *Alysso lusitanici-Santolinetum semidentatae*.

In Portugal, as in other parts in the world, ultramafic landscapes are characterized by a type of rocky and thin soil—leptosol—where large stripped areas are firstly colonized by pioneer perennial species making up grasslands and having a facilitating effect on species of other successional stages (see the phalanx strategy (Lovett Doust 1981). Secondly, shrub formations (*Armerion eriophyllae*), annual grasslands (*Brachypodion distachyi*) and perennial grasslands (*Agrostion castellanae*) form, along with pioneer perennial grasslands, complex mosaics. All such communities developing on incipient soils are very sensitive to the natural succession processes (e.g., shrubbing), facilitated by the absence of wildfire and herbivory.

Most of the obligate serpentinophytes grow in communities of the highly specialized alliance *Armerion eriophyllae*. It is an endemic alliance of the Bercian-Sanabriensean and Lusitan Duriensean biogepgraphical sectors which includes the Meso-supramediterranean silico-basophilic plant communities growing in serpentine habitats. The characteristics and differences between this endemic alliance and the closely related Galician endemic alliance (*Saginion merinoi*) were compiled by Izco and Rivas-Martínez (2018). Mesotrophic perennial grasslands species—i.e., the preferential serpentinophyte *Armeria langei* subsp. *daveaui*—is included in the mesomediterranean, meso-xerophilous and mesotrophic *Armerio daveaui-Agrostietum castellanae*, endemic association that develop in holm oak forest clearings and rocky and thin soils in the Bragança-Vinhais massif (Aguiar et al. 2013). In the rupicolous communities, i.e., *Umbilico violacei-Asplenietum corunnensis* and *Notholaenetum marantae*—are integrated the obligate serpentine relicts *Asplenium adiantum-nigrum* subsp. *corunnense* and *Paragymnopteris marantae*, respectively, both with pregacial origin (low Pliocene) (Aguiar et al. 2011; García-Barriuso et al. 2011b). Such aforementioned communities have a high endemicity in the western Mediterranean basin and, in particular, the Iberian Peninsula (Médail and Verlaque 1997; Aguiar et al. 1998, 2013; Bernardos et al. 2004; Amich and Bernardos 1970).

Worldwide serpentine areas harbour a large number of endemic threatened species regarded as naturally rare species. In the case of Portuguese serpentines, about half of the serpentinophytes (48%) are assigned in some IUCN category: 1 CR (Critically Endangered), 3 EN (Endangered) and 8 VU (Vulnerable) (Table 4). The study performed in southeastern Iberian Peninsula (Andalusia) revealed similar results, that is, 13 obligate serpentinophytes (59%) considered as threatened (Pérez-Latorre et al. 2013). In contrast, only one obligate serpentinophytes out of a total of 11 is considered as EN at a regional level (Selvi 2007).

Portuguese serpentines harbour several endemic taxa and a high number of taxa (more than half) included in some IUCN threatened category. It is important to preserve those populations of widespread and endemic taxa that occur exclusively in Portuguese serpentine areas since they might represent genetically different ecotypes that involve greater genetic diversity and evolutionary fitness of the species (Millar and Libby 1991). Consequently, and in the light of

Table 4. Number of serpentinophytes included in some IUCN red list category.

IUCN red list category	Serpentinophytes	Percentage
CR	1	4
EN	3	13
VU	8	35
LR (NT)	5	22
LR(LC)	6	26
	% serpentinophytes theatened	48

CR, Critically endangered; EN, Endangered; VU, Vulnerable; LR (NT), low risk (near threatened); LR (LC), low risk (least concern).

the aforementioned characteristics, these unique habitats should be considered as priority areas for research and conservation. Likewise, they are important centres of speciation, not only acting as refugia for northern species during the plio-pleistocene glacial cycles generating postglacial neo-endemics (*Odontarrhenaserpyllifolium*, *Antirrhinum rothmaleri*, *Anthyllis vulneraria* subsp. *sampaioana*, *Armeria eriophylla* and *Dianthus laricifolius* subsp. *marizii*) but also like areas that harbour serpentinocolous relict species with pregacial origin (low Pliocene) (e.g., *Asplenium adiantum-nigrum* subsp. *corunnense* and *Paragymnopteris marantae*). Consequently, it is necessary to urgently invert the poor protection that serpentine areas have at present (Kruckeberg 2002, 2004). In Portugal, some areas of ultramafic outcrops are included in the Montesinho Natural Park, but many other areas lack protection. We believe that an adequate measure is to set up a network of Plant Microreserves in order to preserve the floristic and ecological variation of the ultramafic outcrops.

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