Ecological Research

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REVIEW AND SYNTHESIS

Ultramafic Ecology 2025: Proceedings of the 11th International Conference on Serpentine Ecology

Plants of Turkish Ultramafic Areas: Past, Present & Future

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Received: 24 December 2025 | **Revised:** 9 March 2026 | **Accepted:** 16 March 2026

Keywords: edaphic specialization | geoecology | nickel hyperaccumulation | serpentine soils | ultramafic flora

ABSTRACT

Ultramafic (serpentine) soils, derived from magnesium- and iron-rich rocks, impose extreme edaphic conditions characterized by generally low nutrient availability, high Mg:Ca ratios, and elevated concentrations of metals such as Ni, Cr, and Co. These "harsh environments" act as natural laboratories for studying plant adaptation, endemism, and metal tolerance. Türkiye, with its extensive and geologically diverse ultramafic outcrops, harbors one of the richest serpentine floras in the Northern Hemisphere yet remains understudied relative to other regions. This review synthesizes the historical and contemporary understanding of plant life on Turkish ultramafics, tracing early botanical exploration, herbarium-based chemical analyses, and field discoveries that have revealed over 60 Ni-hyperaccumulating taxa and at least 130 serpentine endemics. We highlight how advances in analytical techniques, from portable X-ray fluorescence (pXRF) to molecular and genomic tools, have expanded the detection and ecological interpretation of metal accumulation. Despite this progress, large geographic and taxonomic gaps persist, particularly for central and eastern Anatolia. Future research priorities include comprehensive chemical reanalysis of herbarium specimens, targeted field surveys of unexplored ultramafic regions, integrative molecular–ecophysiological studies to clarify the mechanisms of serpentine tolerance as well as phylogenetic origins of serpentine endemic plants, and applied studies on conservation approaches for Turkish serpentinophytes. Together, these efforts will enhance our understanding of plant evolution in metal-rich environments and contribute to both biodiversity conservation and applied fields such as phytoremediation and biogeochemical prospecting.

1 | Introduction

Many parts of the world contain significant areas of soils derived from ultramafic rocks, rich in ferromagnesian minerals such as olivine, peridotite, dunite, and pyroxene (Garnica-Díaz et al. 2023). Because of the frequent presence of serpentinite (a magnesium silicate mineral) in the soils, they are often referred to as "serpentine soils", and the terms "serpentine" and "ultramafic" are often used interchangeably.

Serpentine soils are typically characterized by low concentrations of essential plant nutrients such as Ca, K, and P, coupled with elevated levels of Mg and elements such as Ni, Cr, and Co. Selective pressures from the unusual soil chemistry can result in floras with reduced species richness compared to surrounding non-ultramafic habitats. Over evolutionary timescales, however, many ultramafic regions have served as centers for endemism and speciation, giving rise to taxa uniquely adapted to these environments. Some serpentine endemics are closely related to species on adjacent "normal" soils and may represent neoendemics derived through local adaptation, whereas others—having diverged long ago—are regarded as paleoendemics (Kruckeberg 2002; Anacker et al. 2011; Kay et al. 2011; Rajakaruna 2018).

Detailed discussion of the serpentine floras of many parts of the world can be found in Brooks (1987), Roberts and Proctor (1992), Baker et al. (1992), Kruckeberg (2002), Rajakaruna et al. (2009), Harrison and Rajakaruna (2011), and Garnica-Díaz et al. (2023). As well as providing information on plant geography, these publications consider in detail the long-recognized chemical and physical challenges imposed on plants inhabiting serpentine soils.

The mechanistic basis of the "serpentine syndrome" or "serpentine factor" remains an active topic of research (Kazakou et al. 2008; O'Dell and Rajakaruna 2011). The principal constraints include: (i) an unfavorable Ca:Mg ratio; (ii) potential toxicity of excess Mg; (iii) toxicity from trace elements such as Ni, Cr, and Co; and (iv) general nutrient poverty, especially P and K deficiency. These edaphic conditions often result in sparse or stunted vegetation, leading to terms such as "serpentine barrens" or "infertile soils." Nonetheless, in many regions, particularly in tropical and Mediterranean ecosystems, ultramafic landscapes support diverse and structurally complex vegetation, enriched by serpentine endemics that complement, rather than merely replace, species from adjacent non-ultramafic areas (Kazakou et al. 2008; Garnica-Díaz et al. 2023). The limited range of specialized studies of the numerous ultramafic exposures of Türkiye has also displayed a remarkable range of serpentine geomorphologies.

2 | History of Turkish Plant Collections

Despite the abundance of ultramafic areas in Türkiye, and of extensive plant collecting since the 16th century, detailed collecting of specimens, specifically from Turkish ultramafics, has been carried out only relatively recently. The very detailed worldwide review by Brooks (1987), for example, includes for Türkiye only the work carried out by Akman (1972) in the Amanos Mountains, where there are extensive exposures of ultramafic soils. It is instructive to note briefly the general history of plant collecting in Türkiye, carried out prior to any work focusing on serpentine areas.

Much of the early interest in Turkish plants came from Western European travelers and was centered on bulbs of ornamental plants and on plants with possible medicinal uses. Significant collections were made by de Tournefort (ca. 1700), and Western Türkiye was visited in the 1780s and 1790s during the epic journeys of Sibthorp, although his main contributions to plant science came from his collections in Greece. In the 18th century, botany underwent development as a pure science, especially with the work of Linnaeus, leading to much more detailed morphological study, species classification, and preservation of specimens in herbaria. During the 19th century, important Anatolian collections were assembled by Aucher-Éloy, Kotschy, von Heldreich, Haussknecht, Balansa, and Sintenis, among others.

Covering a much wider field than Anatolia was the work of Boissier (1867–1884), whose publication of *Flora Orientalis* (1867–1884, with a posthumous supplement in 1888) included more than 4700 species from Türkiye, about half the number recognized now. Since then, further collecting by European botanists has been carried out by people such as Bornmüller, Siehe, and Huber-Morath. Details of the activities of these and other collectors can be found in the extensive article by the late Prof. Asuman Baytop (Baytop 2010).

Most notable, however, was the decision by Peter H. Davis at Edinburgh in 1961 to concentrate the growing body of knowledge by overseeing the recording of all known species in detail in the *Flora of Turkey and the East Aegean Islands*, published in nine volumes (Davis 1965–1985). Davis himself made 11 collecting visits to Türkiye with a number of colleagues, covering much of the country, and contributed almost 30,000 numbered specimens to herbaria at Edinburgh and elsewhere. Subsequent investigations have been carried out by both Turkish and foreign collectors, and supplementary volumes to the Flora were published (Davis et al. 1988; Güner et al. 2000).

Floristic research in Türkiye has progressed rapidly, and alongside newly added checklists and published articles, the release of "Türkiye Bitkileri Listesi: Damarlı Bitkiler [A Checklist of the Flora of Turkey (Vascular Plants)]" (Güner et al. 2012) has provided the most comprehensive compilation of the Turkish flora based on modern taxonomic principles. The volume documents 167 families, 1320 genera, and 11,707 vascular plant taxa, with an endemism rate reported to be approximately 34%.

This remarkable floristic richness has been systematically compiled in Turkish for the first time through the project "Resimli Türkiye Florası [Illustrated Flora of Turkey]", launched in 2014 under the leadership of Turkish botanists. Conceived as a 33-volume, 55-series project incorporating botanical illustrations, it has so far published volumes 1, 2, 3, 4, and 17, along with 9 series. Given that a new plant species is discovered in Anatolia approximately every 10 days, the project represents a significant scientific milestone for Turkish botany by bringing together the region's exceptional plant diversity in a modern, accessible, and nationally produced reference work (Güner et al. 2014).

As in many other countries and regions globally, Türkiye hosts several hundred spatially non-contiguous occurrences of ultramafic geology (Figure 1). It is therefore to be expected that a substantial proportion of the Turkish flora will consist of serpentine-tolerant species ("serpentinophytes"), and that some of these will prove to be serpentine-endemic. By far the greater part of the exploration of the Turkish flora, however, has been carried out without detailed reference to the nature of the substrate from which each specimen was collected.

Ascertaining whether or not a species is "serpentine endemic", from collection records, is difficult because plant collectors of previous centuries have often not mentioned the substrate characteristics. Sometimes, especially in the case of limestone or other calcareous substrates, this is readily apparent, and the collectors' field notes may specify this. Often, however, geological indications are absent, vague, or inaccurate, and locations are not precise enough for any certain conclusion to be drawn. Given that serpentinitic surface environments are derived from igneous mantle material that has forced its way to the surface and then undergone a complex set of physical and chemical processes (Coleman and Jove 1992), recording the geology of a plant collection site using phrases such as "igneous slopes" or "rocky screes" is not particularly informative.

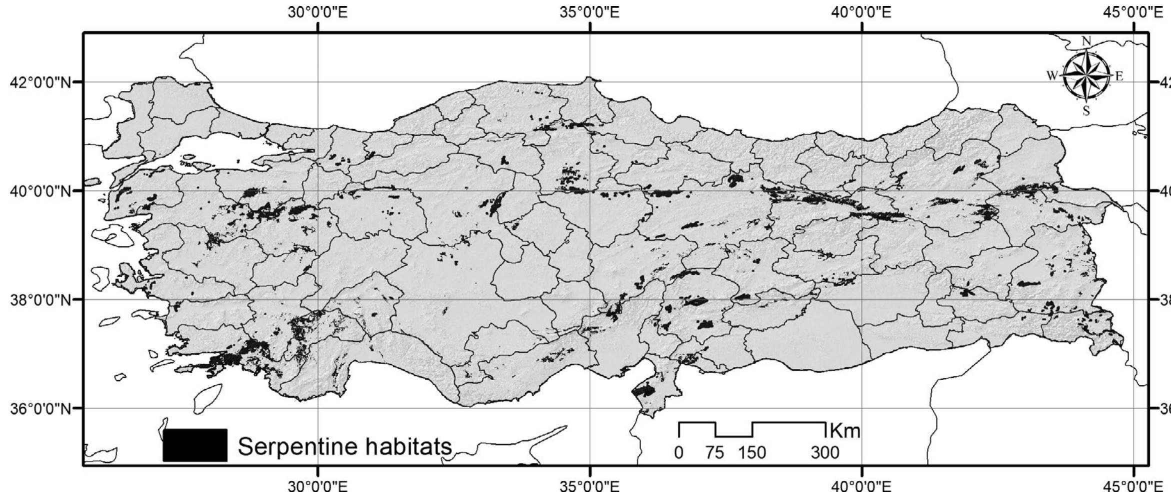

FIGURE 1 | The geographical distribution of ultramafic substrates in Türkiye (Adapted from MTA 2025).

It should also be noted that ultramafic soils, derived from rocks that have undergone a variety of tectonic processes, often occur in close proximity to soils derived from limestones or other calcareous material. Such associations are known from many places, such as Cuba, southeastern Europe, Türkiye, and Japan (Kruckeberg 2002). This proximity can lead to ambiguity in the description of a plant collection site: it may be described as "limestone" when in fact the soil is ultramafic, but the site is marked by the presence of boulders or rubble from nearby limestone cliffs or slopes. In fact, the nature of the soil is not always apparent, even to a field scientist with some geological training, and the degree of its ultramafic composition may only be reliably confirmed through soil analysis.

Although the Introduction in Volume 1 of the Flora of Türkiye (Davis 1965) discusses some geological aspects, there is only a single brief mention of serpentine, and records in the Flora only occasionally indicate that a species is characteristically found on serpentine. There is no doubt, however, that a substantial number of 19th century specimens were incidentally obtained from ultramafics, as such geology constitutes a notable part of many Turkish mountains, mountain ranges, or mountain passes that were visited by collectors. Examples noted on herbarium sheets include the Amanos Mountains (Hatay), Mt. Cassius or Akra Mountain (known today as Keldağ) on the modern border of Türkiye and Syria, Keşiş Mountain (Esence Mts. in Erzincan), Masmeneu or Masmutli Mountain (Niğde province, which includes Hasandağı, Melendiz Mountain, Göllüdağ and the Aladağlar), Sandras Mountain (Muğla), the Dirmil Pass (Burdur), and the Pülümür Pass (Tunceli) (Reeves et al. 2001). In spite of the historical shortage of geological detail, both in the Flora and on herbarium sheets, there has been sufficient recent information to allow a list of 133 probable serpentine-endemic species to be compiled (Adıgüzel and Reeves 2012).

An advance in ascertaining that particular specimens of some species were from serpentine soil came about through the chemical analysis of herbarium specimens. Studies in New Caledonia and other ultramafic regions, including parts of the Mediterranean (Brooks et al. 1977), established that Ni concentrations exceeding 1000 mg kg^{-1} in dry leaf tissue—the accepted threshold for hyperaccumulation—reliably indicate their presence on ultramafic substrates. The investigation of the concentrations of several elements in herbarium specimens of European species of *Alyssum s.l.* (Brooks and Radford 1978) identified 11 species as hyperaccumulators of Ni, in addition to confirming this status in three species in which this behavior was already known. When the study was widened to include all *Alyssum* species worldwide (Brooks et al. 1979), a further 31 species were added to the Ni hyperaccumulator list. All were in section *Odontarrhena* of *Alyssum*, which has now been re-established at the generic level, and widely accepted as such (Španiel et al. 2015). The account by Dudley (1965) indicated that about half of all species of *Alyssum s.l.* recognized at that time occurred in Türkiye, as did half of the species in section *Odontarrhena*. It was therefore not surprising that 26 of the *Alyssum s.l.* Ni hyperaccumulators were species listed in the Flora of Türkiye, even though only four of them are noted there as plants of serpentine. Furthermore, 20 of them were always found with high Ni (although generally from a small selection of fewer than 6 specimens), raising the likelihood that these were in fact serpentine-endemic species. Terminology regarding serpentinophytes as "serpentine obligate" (serpentine endemic) or "serpentine facultative" (not exclusively on serpentine) had been introduced by Novák (1937); it is extensively discussed by Rune (1953) and used by authors such as Borhidi (1991, 1992), Reeves et al. (1999), Kruckeberg (2002), van der Ent et al. (2013), and Pollard et al. (2014).

In certain cases, individuals of a recognized Ni hyperaccumulator species may exhibit foliar Ni concentrations below the 1000 mg kg^{-1} threshold. This variation may arise from several factors. Beyond potential regional genetic differentiation, some species may be serpentine-facultative and collected from non-ultramafic (low-Ni) soils. Alternatively, in serpentine-obligate species, reduced Ni concentrations may reflect local edaphic conditions that limit Ni bioavailability (Reeves et al. 2015).

Further analytical work on herbarium specimens, with a focus on other genera in the Brassicaceae, revealed the existence of Ni hyperaccumulators in the genera *Bornmuellera* (Reeves et al. 1983), *Cochlearia* and *Thlaspi* (Reeves 1988), including species from Türkiye. Many of the relevant *Thlaspi* species are now accepted in the resurrected genus *Noccaea*, and the *Cochlearia* species were transferred first to *Pseudosempervivum* and then to *Noccaea* (Al-Shehbaz 2014; Özüdoğru et al. 2019).

Examples of specimens collected in Türkiye in the 19th century and which were established in the above work as Ni hyperaccumulators (and therefore as plants of ultramafic soils) are given in Table 1. Some of these localities have been the subject of quite intensive later collection throughout the 20th century, but there are probably many areas deserving of further detailed study, as indicated below.

TABLE 1 | 19th century Turkish specimens: Ultramafic substrates deduced from analyses (1978–88) showing Ni hyperaccumulation (*Alyssum, Bornmuellera, Cochlearia, Thlaspi*)[a].

Species	Specimen	Location	Ni conc. (mg/kg)
Alyssum anatolicum (Current: *Odontarrhena anatolica* (Hausskn. ex Nyár.) Španiel, Al-Shehbaz, D. A. German & Marhold)	Sintenis 1889	Sipikor Mt. (Erzincan)	8167
A. cassium (Current: *Odontarrhena cassia* (Boiss. & Heldr.) Španiel, Al-Shehbaz, D. A. German & Marhold)	Post, 11.ix.1884	Amanos Mt. (Hatay)	20,000
A. cilicicum (Current: *Odontarrhena cilicica* (Boiss. & Balansa) Španiel, Al-Shehbaz, D. A. German & Marhold)	Balansa #435, 1855	Güzeldere (Mersin)	13,700
A. crenulatum (Current: *Odontarrhena crenulata* (Boiss. & Heldr.) Španiel, Al-Shehbaz, D. A. German & Marhold)	Boissier, vi.1846	Samandağ (Hatay)	10,390
A. eriophyllum (Current: *Odontarrhena eriophylla* (Boiss. & Hausskn.) Španiel, Al-Shehbaz, D. A. German & Marhold)	Haussknecht, 11.viii.1865	Berit Mt. (Kahramanmaraş)	8531
A. floribundum (Current: *Odontarrhena floribunda* (Boiss.) Španiel, Al-Shehbaz, D. A. German & Marhold)	Balansa #434, 1855	Güzeldere (Mersin)	7706
A. pinifolium (Current: *Odontarrhena pinifolia* (Nyár.) Španiel, Al-Shehbaz, D. A. German & Marhold)	Sintenis #292, 24.iv.1883	Uludağ (Bursa)	9935
A. pterocarpum (Current: *Odontarrhena pterocarpa* (T. R. Dudley) Španiel, Al-Shehbaz, D. A. German & Marhold)	Heldreich #620, 18.v.1845	Çıralı (Antalya)	1190
A. samariferum[b] (Current: *Odontarrhena samarifera* (Boiss. & Hausskn.) Španiel, Al-Shehbaz, D. A. German & Marhold)	Post, 12.vi.1884	Keldağ (Türkiye-Syria Border)	18,900
A. trapeziforme (Current: *Odontarrhena trapeziformis* (Bornm. ex Nyár.) Španiel, Al-Shehbaz, D. A. German & Marhold)	Balansa #431, 8.viii.1855	Masmutli (Niğde)	11,930
Bornmuellera glabrescens (Boiss.) Cullen & T. R. Dudley	Balansa #457	Masmutli (Niğde)	14,800
Cochlearia aucheri (Current: *Noccaea aucheri* (Boiss.) Özüdoğru & Al-Shehbaz)	Sintenis #1267, 5.vii.1889	Sipikor Mt. (Erzincan)	12,070
Thlaspi cappadocicum (Current: *Noccaea cappadocica* (Boiss. & Balansa) Al-Shehbaz)	Balansa #1004, 6.viii.1856	Dededağ (Kahramanmaraş)	24,300
T. elegans (Current: *Noccaea elegans* (Boiss.) Al-Shehbaz)	Post, 6.vii.1884	Keldağ (Türkiye-Syria border)	16,000
T. ochroleucum (Current: *Noccaea ochroleuca* (Boiss. & Heldr.) F. K. Mey.)	Sintenis #277, 1883	Erenköy (Çanakkale)	6050

[a]Nomenclature: *Alyssum* species now transferred to *Odontarrhena*; *Cochlearia* and *Thlaspi* to *Noccaea*.
[b]Collected on Keldağ, on the present-day border of Syria and Türkiye. The mountain was described by Post as a limestone cone on an igneous base; the specimen was named *Peltaria dumulosa* Post, but was later shown by T.R. Dudley to be *Alyssum samariferum* (Reeves et al. 1980).

The herbarium specimen analyses from the 1970s and 1980s reported by Brooks, Reeves, and others led to a program of extensive field exploration, plant collection, plant and soil sampling and analysis, specifically from Turkish serpentine areas, carried out by Reeves, Adıgüzel, and co-workers from 1996 onwards. Collections of more than 700 specimens, made from 55 serpentine sites during 1996–2003, almost all from areas of recorded ultramafic geology (Adıgüzel and Reeves 2012), resulted in further confirmation of the behavior of known Ni hyperaccumulator species, the discovery of new species, rediscovery of very rare species, and identification of further species as Ni hyperaccumulators (Kruckeberg et al. 1999; Reeves et al. 2001, 2009; Adıgüzel and Reeves 2002; Reeves and Adıgüzel 2004). Much of this work, listing 60 Turkish Ni hyperaccumulator taxa, is described in detail in the review of Reeves and Adıgüzel (2008).

Significant collections with a strong focus on serpentine areas of southwest Türkiye were made by Carlström in the 1980s, leading to the description of several new species from the serpentines near Marmaris and elsewhere in Muğla province (Carlström 1985, 1986). These included *Thlaspi cariense* Carlström, now transferred to *Noccaea* (*Noccaea cariensis* (Carlström) Parolly, Nordt & Aytaç) (Aytaç et al. 2006), which has also subsequently been recorded near Lake Köyceğiz (Vural et al. 1995) and in the Sandras Mountain (Reeves and Adıgüzel 2008) and is a hyperaccumulator of Ni (Reeves et al. 2001; Reeves and Adıgüzel 2008). Notable discoveries have also been made in serpentine areas studied less or not at all in earlier centuries. A good example of this is the Kızıldağ area of Konya province near the village of Çamlık, where new species and Ni hyperaccumulators have been found (Aytaç and Aksoy 2000; Aytaç et al. 2006; Reeves and Adıgüzel 2008; Reeves et al. 2009). In fact, eight new taxa have been described from this small area during 2001–2011 (Aytac and Türkmen 2011).

In addition to the above work with a specific focus on ultramafic areas, a number of regional collections by Turkish botanists during the last 60 years have included specimens explicitly stated as being from serpentine or are at least from locations where ultramafic geology is highly probable. This includes the study of the flora of the Beynam Forest (Ankara) by Akman (1972), where ultramafics constitute a significant part of the geology of Kuyrukçu Mountain. Akman provided tables of species for the various communities identified, and those collected from quadrats during vegetation surveys on serpentinitic soils are listed. Later collection and analysis of specimens from the Beynam serpentine included Ni-hyperaccumulating *Thlaspi perfoliatum* L. and the widespread facultative serpentinophyte *Alyssum murale* Waldst. & Kit. (Reeves et al. 2001), species now transferred to *Noccaea* (*Noccaea perfoliata* (L.) Al-Shehbaz) and *Odontarrhena* (*Odontarrhena muralis* (Waldst. & Kit.) Endl.), respectively.

Vural et al. (1995) published an extensive study of species of the Köyceğiz-Dalyan area. Although their primary focus was on phytosociological units, there was recognition of the geology, including sites explicitly noted as serpentinitic. Similarly, a detailed study of the flora of Bakırlı Mountain by Eren et al. (2004) distinguished between sites on the limestone of the cone constituting the upper part of the mountain and serpentine sites of the ophiolitic rocks at lower elevations. The wide-ranging account of Parolly and Eren (2006) also contains a number of references to specimens collected from serpentine or other ophiolitic substrates.

A collection of 1515 specimens from the area of Kızıldağ of Isparta province during 1993–96 has been recorded in some detail (Mutlu and Erik 2003). Only three specimens (*Aethionema arabicum* (L.) Andrz. ex Rchb., *Fibigia eriocarpa* (DC.) Boiss. (*Fibigia clypeata* var. *eriocarpa* (DC.) J. Thiébaut), *Arabis nova* Vill.) are specifically stated to have been collected from serpentine, but from the general geology of the area and the fact that the collection includes several known Ni hyperaccumulators in *Alyssum/Odontarrhena*, such as *Odontarrhena muralis* and *Alyssum peltarioides* Boiss. subsp. *virgatiforme* (Nyár.) Dudley (*Odontarrhena peltarioidea* (Boiss.) Španiel et al. subsp. *virgatiforme* (Nyár.) Španiel et al.), it is likely that the collection includes many other specimens from ultramafic soils.

3 | Turkish Ultramafic Endemics and Red Book Status

From the study of the locations of both field and herbarium specimens, Adıgüzel and Reeves (2012) noted that 133 taxa were by that time believed to be endemic to serpentine soils in Türkiye. Of these, 88 warranted recording of their threat status in the Red Data Book of Turkish Plants (Ekim et al. 2000) in the categories CR (critically endangered, 22 taxa), EN (endangered, 39), VU (vulnerable, 23), and DD (data deficient, 4). In 2021, 73 of the 88 taxa were known only from the single location of the Type specimen; 36 have been recorded as hyperaccumulators of Ni.

Table 2 shows the 22 CR and 4 DD taxa, two of which had their IUCN conservation status changed between 2000 and 2012 (Ekim et al. 2000; IUCN 2000, 2012). Of the 65 species (69 province occurrences) in categories CR, EN, and DD, the provinces that feature most strongly are Muğla (24), Burdur (10), Hatay (9), Adana (5), and Konya (4). Twelve other provinces provide 1, 2, or 3 entries in the list. One of the more remarkable reports since 2000 is that of the rediscovery by Kandemir (2009) of *Onosma discedens* Hausskn. ex Bornm. on serpentine near Salihli (Erzincan), earlier known from an 1890 specimen of Sintenis, but listed in 2000 as EX (i.e., extinct).

New serpentine-associated species described since 2000 almost all warrant placing in one of the most endangered categories, having evaded discovery and/or description for so long. The level of threat needs to be reviewed from time to time. Designation of protected areas can reduce the risk from human activities such as agriculture, mining, and urbanization, but cannot guard against animal damage, insect predation, or forest fire, for example. Two examples, from many recent discoveries, may be mentioned here. *Centaurea aksoyi* Hamzaoğlu & Budak was reported as occurring in four small separate populations on serpentine rocks in Yozgat province, but the area was heavily grazed, justifying CR status (Hamzaoğlu and Budak 2009). *Bolanthus sandrasicus* Hamzaoğlu & Koç (*Jordania sandrasica* (Hamzaoğlu & Koç) Rabeler & Madhani) was described by Hamzaoğlu et al. (2017) in the Sandras Mountains (Muğla); it is found only within an area of 1 km^2, is also threatened by

TABLE 2 | Threatened Turkish Serpentine Endemics (IUCN Categories CR and DD) and maximum Ni concentrations.

Family	Species	Province	Category	Max. Ni (mg/kg)
Asteraceae	*Anthemis karacae* Güner	Muğla	CR	NA
Asteraceae	*Centaurea aladaghensis* Wagenitz	Adana	CR	9900
Asteraceae	*Centaurea arifolia* Boiss.	Hatay	CR	22,500
Asteraceae	*Centaurea doddsii* Post ex Boiss.	Hatay	DD	NA
Asteraceae	*Centaurea ensiformis* P. H. Davis	Muğla	CR	37,750
Asteraceae	*Centaurea foliosa* Boiss. & Kotschy (*Centaurea zaferii* Negaresh)	Hatay	CR	NA
Asteraceae	*Centaurea kizildaghensis* Uzunh., E. Doğan & H. Duman	Konya	CR	NA
Asteraceae	*Centaurea ptosimopappoides* Wagenitz	Adana	CR	11,660
Asteraceae	*Centaurea sericea* Wagenitz	Balıkesir & Eskişehir	DD	14,830
Boraginaceae	*Rindera dumanii* Aytaç & R. R. Mill	Konya	CR	NA
Brassicaceae	*Alyssum davisianum* T. R. Dudley (*Odontarrhena davisiana* (T. R. Dudley) Španiel et al.)	Kütahya	CR	19,570
Brassicaceae	*Alyssum syriacum* Nyár. (*Odontarrhena syriaca* (Nyár.) Španiel et al.)	Hatay	DD	10,190
Brassicaceae	*Bornmuellera kiyakii* A. Duran & Hamzaoğlu	Konya	CR	12,590
Brassicaceae	*Hesperis kuerschneri* Parolly & Kit Tan	Denizli	CR	NA
Brassicaceae	*Thlaspi rosulare* Boiss. & Balansa (*Noccaea rosularis* (Boiss. & Balansa) Al-Shehbaz)	Niğde	CR	31,940
Caryophyllaceae	*Gypsophila graminifolia* Barkoudah	Van	CR	NA
Caryophyllaceae	*Herniaria amoena* Çeleb. & Favarger	Adana	EN → CR	NA
Colchicaceae	*Colchicum lingulatum* subsp. *rigescens* K. Perss	Muğla	CR	NA
Colchicaceae	*Merendera figlalii* Varol (*Colchicum figlalii* (Varol) Parolly & Eren)	Muğla	CR	NA
Fabaceae	*Astragalus serpentinicola* H. Duman & Ekim	Burdur	VU → CR	NA
Fabaceae	*Chamaecytisus gueneri* H. Duman, Başer & Malyer (*Cytisus gueneri* (H. Duman, Başer & Malyer) Vural)	Muğla	CR	NA
Fabaceae	*Ebenus pisidica* Hub.-Mor. & Reese	Burdur & Muğla	CR	NA
Rubiaceae	*Galium setuliferum* Ehrend. & Schönb.-Tem.	Adana	DD	NA
Scrophulariaceae	*Verbascum dudleyanum* (Hub.-Mor.) Hub.-Mor. *(Verbascum pyroliforme* subsp. *dudleyanum* (Hub.-Mor.) Karavel. & Aytaç)	Burdur	CR	NA
Scrophulariaceae	*Verbascum flabellifolium* (Hub.-Mor.) Hub.-Mor. (*Verbascum trapifolium* var. *flabellifolium* (Hub.-Mor.) Karavel. & Aytaç)	Burdur	CR	NA
Scrophulariaceae	*Verbascum serpenticola* (Hub.-Mor.) Hub.-Mor.	Burdur	CR	NA

Abbreviations: CR: Critically Endangered; DD: Data Deficient; EN: Endangered; VU: Vulnerable; NA: Data not available.

grazing, and has been placed in the EN category. In a few cases, the threat level can be reduced by the discovery of new populations of a known species, but more often the threat continues to escalate, owing to increases in agriculture and planted forestry, urbanization, and fire.

4 | Current Work

Although ultramafic studies in Türkiye date back several decades, research has accelerated significantly as awareness of the ecological importance of these habitats has grown.

4.1 | Floristics, Taxonomic, and Endemism-Focused Studies

Serpentine soils are recognized as key habitats within many of Türkiye's Important Plant Areas (IPA 15, 34, 35, 38, 46, 48, 50, 52, 53, 55) owing to their distinctive and highly specialized plant groups (Avcı 2005; Özhatay et al. 2005). Research highlights Muğla as a major serpentine diversity center, with notable hotspots at Sandras Mountain, Marmaris–Köyceğiz, and Datça (Yeşilyurt and Akaydın 2012), and further serpentinophytic communities identified in the Western Taurus (Parolly 2021).

Additional concentrations of serpentine-associated species are documented at Phaselis (Göktürk 2015), Mount Dedegül (Özçelik 2018), Denizli (Çelik et al. 2004; Çiçek and Çon 2022), and across the Aydın–Muğla–Denizli region, where several endemics show climate sensitivity (Sütgibi 2025). Western Anatolian sites such as Murat Mountain (Keser 2013), the Büyükorhan–Harmancık region (Bağçıvan and Daşkın 2019), and parts of Kastamonu in the Western Black Sea region (Güney et al. 2015) also exhibit strong links between ultramafics and endemism. In Central and Eastern Anatolia, serpentine soils structure plant distributions in Çankırı (Dölarslan et al. 2017, 2018) and occur widely across the Palandöken, Munzur, Taurus, and Amanos ranges (Öztürk et al. 2015; Türkmen 2018). Erzincan's serpentine zones are particularly important, concentrating many threatened taxa and hosting rediscoveries such as *Verbascum calycosum* Hausskn. ex Murb. (Kandemir et al. 2015, 2022).

Türkiye has produced many new serpentine-derived taxa, including early discoveries such as *Ekimia bornmuelleri* (Hub.-Mor. & Reese) H. Duman & M. F. Watson, *Colchicum figlalii* (Varol) Parolly & Eren, *Hesperis kuerschneri* Parolly & Kit Tan, *Hesperis ozcelikii* A. Duran, *Silene nerimaniae* G. E. Genç, Kandemir & I. Genç, *S. dumanii* Kandemir, G. E. Genç & I. Genç, and *Centaurea serpentinica* A. Duran & B. Doğan (Duman and Watson 1999; Parolly and Tan 2006; Genç et al. 2007; Parolly and Eren 2007; Duran 2009; Doğan and Duran 2009; Kandemir et al. 2009).

Later additions include *Allium serpentinicum* I. Genç & Özhatay, *A. kandemirii* I. Genç & Özhatay, *Onosma atila-ocakii* O. Koyuncu & Yaylacı, *Dianthus serpentinus* Hamzaoğlu, *Muscari elmasii* Yıldırım, and *Galium cariense* Daşkın & Bağçıvan (Genç and Özhatay 2013; Koyuncu et al. 2013; Hamzaoğlu et al. 2015; Yıldırım 2016; Daşkın and Bağçıvan 2017).

Updated assessments expanded the serpentine flora of Türkiye to 248 taxa, mostly endemic (Özdeniz et al. 2017). Newly described serpentine taxa continue to accumulate across the country, e.g., *Ekimia ozcan-secmenii* Şenol & Eroğlu, *Scutellaria topcuoglui* Yıldırım, Çiçek & Akbaş, *Satureja hasturkii* H. Duman & Dirmenci, *Noccaea anatolica* Sefalı, Yapar & Demir, *Onosma koruklueі* Aytaç, Ertuğrul & Fişne, *Allium decumbens* Balos & Sonay, *Onosma serpentinica* Yıldırım & Binzet, *Fritillaria ozgeana* H. Duman & Tekşen, *Pimpinella husnucan-baseri* Duran, *Allium serpenticola* Eker, *Bolanthus sertavulus* Özçelik, *Cyclotrichium tulayae* Başköse & Savran, *Ferula erzincanica* Sağıroğlu, H. Duman & B. Bani, and *Onosma guniae* Binzet (Şenol and Eroğlu 2018; Yıldırım et al. 2021; Duman et al. 2023; Sefalı et al. 2023; Aytaç et al. 2023; Balos and Sonay 2024; Binzet et al. 2024; Duman and Tekşen 2024; Duran et al. 2025; Eker 2024; Özçelik 2024; Başköse et al. 2025; Sağıroğlu et al. 2025; Binzet 2025). Additionally, *Muscari commutatum* Guss. was newly recorded on serpentine in Türkiye (Uysal et al. 2021). Across all regions, serpentine habitats remain focal points for continued morphological, physiological, ecological, and genetic research on Türkiye's specialized flora.

4.2 | Studies on Metals and Hyperaccumulation

Surveys across Türkiye have revealed numerous serpentine-associated hyperaccumulators and metal-tolerant taxa. In the Mersin Fındıkpınarı–Erdemli region, several *Alyssum* species were shown to accumulate high concentrations of Ni (Özdemir and Demir 2010). Further studies identified new Ni-hyperaccumulators, including *Noccaea camlikensis* A. Duran & Aytaç, *Bupleurum croceum* Fenzl, and confirmed the strong accumulation capacity of known taxa such as *Alyssum caricum* T. R. Dudley & Hub.-Mor. (*Odontarrhena carica* (T. R. Dudley & Hub.-Mor.) Španiel et al.), *Odontarrhena peltarioidea*, *O. muralis*, *Bornmuellera kiyakii* Aytaç & A. Aksoy, and *Alyssum pateri* subsp. *pateri* Nyár. (*Odontarrhena pateri* (Nyár.) Španiel et al.) (Altınözlü et al. 2012; Aksoy et al. 2015, 2017; Sağlam 2017; Çelik et al. 2018; Özbey 2019; Dindaroğlu et al. 2019). Additional discoveries include Zn accumulation in *Viola kizildaghensis* Yıldırım, Hamzaoğlu & Koç (Aksoy 2021) and high Co, Fe, and Ni uptake in plants from mining areas, with *Odontarrhena muralis* confirmed as both a strong Ni and B accumulator and *Teucrium polium* L. as an accumulator of Sr. (Kılıç and Ortakçı 2021; Konakçı et al. 2023; Konakçı and Şaşmaz 2024; Konakçı 2024). In Muğla–Köyceğiz, several endemics showed pronounced metal tolerance, including Ni hyperaccumulation in *Alyssum masmenaeum* Boiss. (*Odontarrhena masmenaea* (Boiss.) Španiel et al.) (Yıldıztekin et al. 2024). Soil studies from the Burdur–Gölhisar basin indicate that Ni–Cr levels are quite high; however, pH and lime content reduce the effects of metal toxicity in plants, and such serpentine soils may even support cultivation under suitable conditions (Altunbaş 2019, 2023).

Defining a species as an accumulator is a decision requiring careful consideration, and additional work is required to confirm these findings. High concentrations can be verified by scanning herbarium specimens using portable X-ray fluorescence (pXRF). However, beyond its limited sensitivity, scanning herbarium material with pXRF is not a complete solution, because (i) we generally do not know the full history of a specimen from collection to mounting in the herbarium, and (ii) herbarium specimens are almost certainly not washed to analytical standards; therefore, the issue of soil contamination still remains for in situ herbarium analyses. Ultimately, the most reliable work comes from competent researchers who not only fully understand the analytical instrument technology but also oversee the entire process, starting from the collection itself.

4.3 | Other Studies

Studies across Türkiye, especially in Erzincan and Central Anatolia, demonstrate that serpentine substrates exert strong selective pressures shaping plant morphology, physiology, and chemistry. Morphological differentiation between serpentine and non-serpentine populations has been documented in *Scrophularia subaequiloba* Lall (Türkmen and Kandemir 2014) and *Onosma argentata* Hub.-Mor. (Özkan et al. 2016). Elemental analyses show distinct substrate-based signatures and high regional endemism, with serpentine taxa exhibiting elevated antioxidants (Osma and Kandemir 2016; Varol et al. 2023; Şimşek et al. 2025). Physiological studies reveal species-specific stress responses in serpentine plants. While many species accumulate soluble carbohydrates, proline, and phenolic content vary considerably among taxa. In some species, serpentine populations exhibit elevated chlorophyll a concentrations accompanied by variable chlorophyll b levels, further supporting the existence of multiple adaptive strategies (Özbey et al. 2017; Çınar et al. 2021; Albayrak-Çekiç et al. 2021). Mechanisms of metal tolerance differ even within genera, as shown by contrasting proteasome responses in *Alyssum* species and confirmed genetic stability in the hyperaccumulator *A. caricum* (*Odontarrhena carica*) (Van Hoewyk et al. 2018; Çördük and Yücel 2023). Soil comparisons further highlight the strong influence of parent material on nutrient cycling and microbial processes (Sağlıker et al. 2018). Phylogenetic studies emphasize the tight serpentine association of endemic lineages such as *Bornmuellera* (Okan et al. 2024) and the contrasting ecological specializations of *Scrophularia fatmae* Kandemir & İlhan and *S. erzincanica* R. R. Mill (Yıldız et al. 2023, 2024, 2025). Overall, serpentine habitats act as powerful drivers of diversification, endemism, and specialized physiological strategies in the Turkish flora.

5 | Proposals for Future Work

Future work designed to advance our knowledge and understanding of the Turkish serpentine flora can be considered under three general headings: (1) further chemical analysis of existing herbarium specimens; (2) field-based studies involving exploration, plant and soil collection, plant identification and plant and soil analysis; and (3) laboratory-based work, including (i) greenhouse studies from a variety of seed collections, to investigate plant behavior under controlled conditions, and (ii) genomic studies to investigate interrelationships among various taxa.

1. Our present knowledge of Ni hyperaccumulation in the Turkish serpentine flora was based initially on herbarium specimen analysis of small leaf fragments, followed in some cases by locating additional specimens in the field. The plant tissue analysis has been accompanied in some cases by soil sampling and analysis to establish the nature of the substrate more precisely.

Although *Odontarrhena* species have received considerable attention, several issues still warrant further investigation of herbarium material, particularly with access to recent advances in highly sensitive, non-destructive pXRF instrumentation and other methods (Purwadi et al. 2021). Ideally, such analyses should not only identify specimens with Ni concentrations exceeding 1000 mg kg^{-1} but also provide reliable measurements down to approximately 10–20 mg kg^{-1}. Further investigation of Ni accumulation is needed in several genera. In both *Odontarrhena* and *Centaurea*, some species exhibit a wide range of Ni concentrations, including values both above and below the hyperaccumulator threshold, possibly reflecting their serpentine-facultative distribution. Of the 172 Turkish *Centaurea* species recorded by Wagenitz (1975), only a subset have been analyzed for Ni accumulation; additional taxa listed in that account, as well as species described subsequently—some of them potentially rare—are likely to be serpentine-endemic or at least serpentine-facultative and therefore warrant investigation. Further study is also required in genera such as *Noccaea* and *Aethionema*, in which Ni accumulation is already well established in certain species. In *Noccaea* in particular, careful re-examination of herbarium material may be necessary, given the extensive taxonomic revisions the genus has undergone in recent years (Özüdoğru et al. 2019).

2. Many areas in Türkiye that are indicated on geological maps as locations of peridotite, serpentinite, "ophiolite", or other ferromagnesian rock types do not appear to have been extensively explored botanically. There are also substantial areas of "ophiolitic mélange" (mixtures of ultramafic materials with several other kinds). These are less likely to support a characteristic serpentine flora but could nevertheless be worth a brief study.

Reeves, Adıgüzel, and associates during 1996–2003 recorded visits to 55 ultramafic sites covering a wide geographic area, from Çanakkale and Muğla provinces in the west, to Ankara, Niğde, and Konya in the centre, and further east to Tunceli, Erzincan, and Hatay. However, the study of each site was somewhat superficial, sometimes involving a stay of as little as half an hour, and never more than 2 days. Nevertheless, this work included the discovery of new species, the rediscovery of several species collected by only a single collector during the 20th century, additions to the distribution range of some species, and new data on Ni hyperaccumulation by many of the 60 Turkish species that show this behavior. This suggests that there is almost limitless opportunity for further detailed study of Turkish ultramafic sites.

Such studies could include more exploration of areas already noted for collections dating back to the 19th century, but which are very extensive, such as the Amanos Mountains, areas around Marmaris, and elsewhere in Muğla province, such as Sandras Mountain, the Pülümür Pass (Tunceli), the east–west occurrences from east of Erzincan city to west of Refahiye (Erzincan), the Dirmil Pass (Burdur), and the Kütahya-Tavşanlı area. However, in recent times, significant discoveries have also been made in areas less studied in earlier centuries.

Despite two centuries of intensive botanical collecting, provinces such as Erzincan continue to yield new species, many of them restricted to ultramafic substrates. Collection histories, from early single-record collectors to major contributors like Sintenis, Davis, and especially Kandemir, show extensive sampling, yet still overlook important sets of specimens, including ultramafic collections by Reeves and Adıgüzel. Given Erzincan's large serpentine areas and known Ni-hyperaccumulating flora, many past specimens undoubtedly originate from ultramafic habitats. Ongoing serpentine-focused research continues to uncover new taxa (Gemici et al. 2008; Kandemir 2009; Aytaç et al. 2015; Binzet 2025), suggesting that the roughly 180 species first described from Erzincan (Kandemir and Yıldız 2016) will likely increase further.

The apparent importance of provinces such as Muğla, Hatay, and Erzincan for Turkish serpentinophytes may be partly a reflection of their large areas of ultramafic geology, and partly due to the intensity of plant exploration there, over more than 150 years. Several approaches to further exploration are also likely to be fruitful. The majority of past collections have been conducted in areas near roadways or along trails leading toward the summits of major mountains. Even in well-explored provinces, there are still possibilities for new discoveries (i) by venturing well off "the beaten track", and (ii) by making visits at times of the year when exploration has been less common (e.g., in early spring).

Several extensive ultramafic regions in Türkiye remain underexplored and are likely to yield further botanical discoveries. Notable examples include large peridotite and ophiolitic mélange formations at the Bayburt–Erzincan–Erzurum border, broad ophiolitic zones in the Lakes District and around Konya, and the Salda Lake area, where ultramafics extend beyond currently collected areas. Additional under-sampled provinces with significant ultramafic geology include Balıkesir, Bursa, Denizli, Gümüşhane, Niğde, and Sivas. Comprehensive geological syntheses by Yılmaz and Yılmaz (2013) and Parlak (2016) highlight further promising areas for ultramafic-focused plant exploration.

3. Future laboratory-based work on serpentinophytes can take several forms, but is centered on increasing the understanding of the morphology, genetics, and ecology of particular species. Ecological studies derived from field observation and sample collection include chemical analysis of plant and soil materials from the field, as well as subsequent plant growth experiments under controlled conditions.

There are instances from herbarium collections where specimen identification has been difficult because there are no significant morphological differences between the specimen and the circumscription of the nearest likely species. In such cases, further collection, followed by micromorphological examination and DNA analyses, may allow a determination of whether the establishment of a new taxon is justified. Examples of "erratic" or inconsistent Ni hyperaccumulation could also be followed up through further specimen collection and laboratory studies to elucidate the causes of the variable behavior.

6 | Conclusions

Türkiye contains some of the world's most numerous and notable ultramafic areas, with landscapes that are extensive, heterogeneous, and exceptionally informative for understanding how edaphic stress drives plant diversification. The synthesis of historical collections, herbarium-based geochemical screening, and recent fieldwork reveals a flora rich in serpentine endemics and at least 60 confirmed Ni hyperaccumulators, yet major portions of the country, particularly central and eastern Anatolia, remain undersampled. Ultramafic systems in Türkiye thus offer a powerful model to link nutrient limitation, metal tolerance, and physiological specialization with patterns of endemism and community assembly. Future progress hinges on three complementary advances: broad application of non-destructive, high-sensitivity elemental screening to herbarium specimens; coordinated, hypothesis-driven surveys of unmapped ultramafic exposures and ophiolitic mélanges; and integrative molecular, isotopic, and imaging approaches to resolve uptake, transport, and sequestration mechanisms and their evolutionary origins. Given ongoing pressures from land use, mining, and fire, conservation planning should prioritize narrow-range endemics and habitat mosaics spanning ultramafic–non-ultramafic ecotones. Cross-disciplinary collaboration across geology, soil science, ecology, and evolutionary biology will be essential to transform Türkiye's ultramafic landscapes into a globally comparative framework for both basic and applied research.

Acknowledgments

The authors sincerely thank Prof. Ahmet Mert (Isparta University of Applied Sciences, Türkiye) for his valuable contribution in preparing the map used in this study. We are also grateful for the constructive comments we received from two anonymous reviewers and the handling editor.

Conflicts of Interest

Nishanta Rajakaruna is an Associate Editor-in-Chief for the special issue on Serpentine Ecology and had no part in the peer review and decision-making processes for this paper.

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