Article

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The genus *Limonium* (*Plumbaginaceae*) in Tunisia: taxonomy, biogeography and conservation

Abstract

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The recent increase in the known richness of Limonium in Tunisia, mainly due to the description of 25 new endemic species in the last decades, has made the only existing identification key for the country obsolete. Based on an exhaustive review of the literature dealing with *Limonium* from Tunisia, consultation of herbarium specimens preserved in Tunisia and Sicily, and a number of new collections, we propose here a new complete key, accompanied by an updated mapping for all taxa. The obtained results reveal that most Tunisian *Limonium* are perennial herbs (81 %), halophytes (79 %), endemic to the country (61 %), and mainly distributed along coasts and around chotts. A significant number of taxa (51 %) present important conservation issues, mainly related to microendemism (especially on islands and peninsulas) and to the alarming acceleration of habitat degradation. Djerba Island is currently the subject of a project involving local authorities, residents and environmental protection associations aimed at conserving the microendemic *Limonium formosum*, whose only location is threatened in the short term by a project to turn it into a tourist attraction.

Key words: North Africa, halophilous vegetation, endemism.

Introduction

The genus *Limonium* Mill. (Plumbaginaceae) is extremely variable, diversified and complex, as a result of its high degree of agamospermy, polyploidy, hybridization and polymorphism (Cowan & al. 1998; Palop-Esteban & al. 2007). Its phylogeny is consequently still partially resolved (Lledo & al. 2005). The first classification attempts were conducted by Boissier (1848, 1859) who considered it under the name *Statice* L. Rechinger (1936, 1938, 1943), in his work on the Aegean region, was one of the first authors to transfer *Statice* species into the genus *Limonium* (Brullo & Erben 2016). Subsequently, the name *Statice* was definitively considered invalid by Greuter & al. (2000). Thanks to molecular and phylogenetic investigations, the conception of the genus *Limonium* has

evolved during the last decades, resulting in the transfer of some species into various small genera, such as *Acantholimon*, *Goniolimon* or *Myriolimon* (Lledo & al. 2005). To date, *ca.* 600 taxa have been described (Koutroumpa & al. 2018), most of which being concentrated in the Mediterranean Basin (Greuter & al. 1989). This region, which houses about 70 % of the known species and most of the stenoendemics, appears as the biodiversity center of the genus (Koutroumpa & al. 2021).

In North Africa, including Macaronesia, Dobignard & Chatelain (2013) reported 107 taxa, among which 69 are endemic to a single country. However, these assessments are highly dependent on field survey efforts and taxonomical studies conducted over the past decades. Indeed, *Limonium* richness of Greece, which was once estimated at 15 taxa by Pignatti (1972), was recently increased to 85 species by Brullo & Erben (2016)! The same comparison made in the three Maghreb countries (Table 1) reveals that only Tunisia has been recently investigated, and that the small changes reported for Algeria and Morocco were a result of taxonomical modifications. In Tunisia, Brullo & Erben (1989) distinguished 36 species, among which 21 were new for science. Other taxa were discovered or described later, such as *L. comosum* Erben, *L. formosum* Bartolo, Brullo & Giusso, *L. elfahsianum* Brullo & Giusso del Galdo and *L. steppicum* Sefi, Ghrabi-Gammar & Brullo (Erben 2001, Bartolo & al. 2003, Brullo & al. 2006, Sefi & al. 2020). One species, formerly recognized as *Limonium ferulaceum*, has been transferred to the genus *Myriolimon*. Accordingly, these recent changes radically alter the knowledge of the genus *Limonium* in Tunisia, and seriously complicate the identification of species in the field.

Moreover, as the variability and diversity of *Limonium* are strongly linked to geographical and ecological isolation, most species of this genus occur in rather peculiar habitats, such as rocky coasts and salt marshes (Brullo & Erben 2016). The recent field surveys conducted by the authors (Ghrabi-Gammar & al. 2020; Ben Charfi & Numa 2021) have highlighted several types of threats, which currently weigh on fragile biotopes with high conservation challenges. Most regions do not benefit from any protection status and are subject to an accelerated loss of habitats, likely to lead to the extinction of several *Limonium* species in the near future.

The aims of the current study are: (1) to give an updated identification key based on the state-of-art regarding taxonomy, nomenclature and chorology of Tunisian *Limonium*, (2) to provide distribution maps for all *Limonium* taxa of Tunisia, and (3) to assess the threat sta-

Table 1. Richness in taxa and strict endemics of *Limonium* in the three Maghrebi countries, from Quézel & Santa (1963), Aimé & Roiron (1985), Pottier-Alapetite (1981), Fennane (1999) and Dobignard & Chatelain (2013).

		Taxa	Strict endemics
Algeria	1963-1985	27	9
	2013	28	5
Morocco	1999	34	10
	2013	36	12
Tunisia	1981	18	1
	2013	42	26

tus of *Limonium* taxa at the national scale, and present an example of conservation actions for *L. formosum*, a critically endangered microendemic from Djerba Island.

Material and methods

Identification key

Apart from the partial key of *Limonium steppicum* and its allied species present in Djerba (Sefi & al. 2020), no recent key including the newly described species has been established yet. Thus, we propose in the current work a complete identification key of *Limonium* taxa occurring in Tunisia and so far, recognized. In so doing, and in order to fully grasp the diacritic characters of the different *Limonium* species, we extracted all available data from literature. Moreover, we ascertained and completed missing measurements by careful examination of 110 samples collected in different regions of Tunisia (Kroumiria, Northeast, Center and South, including the island of Djerba) and kept at the herbarium of the *Institut National Agronomique de Tunisie* (INAT), as well as those of the herbarium specimens of 41 *Limonium* species, consulted at the herbarium of the University of Catania, Sicily (CAT). Insofar, as the geographic isolation is a major cause of speciation in the genus, geographic criteria were also used for taxa identification (Tison & De Foucault 2014; Brullo & Erben 2016). Endemism and distribution areas are consequently specified for stenoendemic taxa. Endemism status was determined from available literature as well as online databases, such as *Plants of the World Online*, *African Plant database*, *eflora Maghreb* and *Euro+Med Plantbase*. Finally, according to the biogeographical distribution of *Limonium* species, four levels of endemism were identified: exclusive to Tunisia (T), shared between two countries, in our case Algeria-Tunisia (AT), related to at least three North African countries (NA) and on a larger scale, *i.e.* Mediterranean and beyond (Med). The nomenclature of the taxa was updated according to Dobignard & Chatelain (2013), Le Floc'h & al. (2010) and Domina & El Mokni (2019).

Status assessment

In Tunisia, the *Code forestier* (Anonyme 2012) is the main legislative text promulgated for the protection of rare and threatened taxa of wild flora and fauna, as well as those covered by international treaties (Khabbach & al. 2021). Nevertheless, this code refers more specifically to forest-dependent taxa and therefore could not ensure adequate protection of those that thrive in other habitats or ecosystems. Furthermore, there is the so-called *Registre National des Espèces Sauvages* (REGNES; Anonyme 2010), established in 2010 thanks to the support of IUCN, but including only *ca.* 50 species of birds, emblematic for their number or conservation status, and *ca.* 100 plant taxa.

Likewise, the authors were actively involved, under the aegis of IUCN, in the threat status assessment, at the Mediterranean scale, of some Tunisian Monocotyledonous taxa and others occurring more particularly in freshwater wetlands (e.g. García & al. 2010). Nonetheless, it is worth mentioning that so far, no taxa of the genus *Limonium* occurring in Tunisia, have been assessed in the IUCN Red List of threatened species. Even the National Red List of Tunisia,

which is being devised, is dedicated only to the avifauna and to some groups of the flora, namely *Lycopodiophytes*, *Polypodiophytes*, Gymnosperms and Monocotyledons.

Data were collated as exhaustively as possible from the available literature (e.g., Pottier-Alapetite 1981; Brullo & Erben 1989, 2016; Erben 2001; Bartolo & al. 2003; Brullo & Giusso del Galdo 2006; Pavon & Véla 2011; Tison & De Foucault 2014; Greuter & Domina 2015; Médail & al. 2015; Erben & al. 2018; Gamoun 2020; Sefi & al. 2020), from herbarium samples preserved at INAT, including those from P. Leboulenger's personal collection, from harvesting samples mentioned in the *eFlora Maghreb* database and from field surveys conducted by the authors. Historical stations were considered for the calculation of the area of occupancy (AOO) and the extent of occurrence (EOO). These areas were computed using the GeoCAT tool developed by RBG Kew. The locations were grouped according to the physiographic subdivisions of Tunisia, defined by Cuénod & al. (1954).

This thorough literature analysis, underpinned by field surveys, has allowed us to build a sufficiently complete dataset to calculate the values of AOO and EOO, and to determine the categories and criteria justifying the assessment of the conservation status of *Limonium* taxa. The geolocation data allowed us to establish biogeographical distribution maps of the different taxa, but more particularly of the stenoendemic ones. These maps were created using QGIS 3.16.

Phylogeny

Based on the phylogenetical studies by Lledo & al. (2005) and Koutroumpa & al. (2018), 10 of the 43 taxa occurring in Tunisia can been assigned to the infrageneric subdivisions recognized by Koutroumpa & al. (2018). They belong to the following clades:

Subgen. *Pteroclados* (Boiss.) Pignatti *s.l.* Generally perennial herbs, with entire or sinuated basal leaves; stems often bearing wings; spikelets distichous; calyx infundibuliform; corolla often white, sometimes yellow or light pink; fruit with circumscissile dehiscence (Karis 2004; Koutroumpa & al. 2018).

Sect. *Pteroclados*. Species of the sect. *Pteroclados* differ chemically from all other *Limonium* by producing glycine betaine but not ßalanine betaine (Hanson & al. 1994).

Subsect. *Odontolepideae* (Boiss.) Koutroumpa. This subsection, mostly distributed in the Mediterranean region, is opposed to the sect. *nobile* endemic of Macaronesia, and is characterized by cuspidate inner bracts and usually conspicuously winged stems (Karis 2004). In Tunisia, it comprises *L. bonduellei*, *L. lobatum* and *L. sinuatum*.

Subgen. *Limonium*

Sect. *Limonium*. Perennial herbs reaching 15 to 150 cm; leaves large, pinnately veined, organized in basal rosette; sterile branches few or absent; inflorescence with more or less dense spikes; spikelets small, usually with 1-4 flowers; calyx obconical or very narrowly funnel-form; calyx limb short, undulate, bearing 5-10 distinct lobes, usually with short lobes placed between larger lobes; corolla bluish-violet, rarely lilaceous. This section, understood here in the restricted conception of Koutroumpa & al. (2018), comprises *L. boitardii* and *L. narbonense*.

Sect. *Nephrophyllum* Rech.f. *s.l.* (including species of the sect. *Limonium* subsect. *Hyalolepideae*, i.e. part of the '*L. bellidifolium* complex'; Koutroumpa & al. 2018).

This section comprises only Irano-Turanian elements, with the notable exception of *L. bellidifolium*, which is present in Tunisia. It is characterized by rosette leaves disappearing during flowering, amplexicaule or semi-amplexicaule stem leaves (sometimes absent), generally present sterile branches, and numerous small spikelets with broadly membranous (hyaline) outer and inner bracts (Boissier 1848; Akhani & al. 2013; Erdal 2015; Malekmohammadi & al. 2017).

Sect. *Pruinosum* (Batt.) Koutroumpa. This section is characterized by stems and branches covered by calcariferous tubercles with a central punctuate depression, numerous sterile branches, one-flowered spikelets, calyces with membranous limbs, and deciduous leaves (Koutroumpa & al. 2018). In Tunisia, it comprises *L. allezettei* and *L. pruinosum*.

Sect. *Schizhymenium* (Boiss.) Bokhari. This section encompasses annual species bearing characteristic subtubular calyces with limbs lacerating at maturity and ribs forming more or less hooked barbs (Bokhari 1972). In Tunisia, it comprises *L. avei* and *L. echioides*.

Key of Tunisian *Limonium*

The key of Tunisian *Limonium* integrates classic criteria concerning longevity (annual vs perennial), stems (winged versus not winged, with or without tubercles), occurrence of sterile stems, leaves (color, shape, margin, apex), inflorescences (size, shape, spikes, spikelets, bracts) and flowers (size and color of calyx and corolla) (e.g. Brullo & Erben 2016). The values and modalities of the used criteria were extracted from Pottier-Alapetite (1981), Brullo & Erben (1989), Erben (2001), Bartolo & al. (2003), Brullo & Giusso del Galdo (2006), Tison & De Foucault (2014), Erben & al. (2018) and Sefi & al. (2020). Endemism and distribution areas are specified for stenoendemic taxa. The used nomenclature follows Brullo & Erben (1989), Erben (2001), Le Floc'h & al. (2010) and Sefi & al. (2020). Endemism is indicated between square brackets after species names: A, Algeria; L, Libya; M, Maghreb; T, Tunisia.

1 Stems winged; leaves sinuate (subgen. *Pteroclados*) **2**
1 Stems not winged; leaves entire or absent (subgen. *Limonium*) **4**
2 Calyx divided in 5 acute lobes alternating with 5 ridges; leaves mucronate; spikelet < 10 mm; annual ..... ***L. lobatum***
2 Calyx nearly undivided, truncated serrated; leaves rounded; spikelet > 10 mm; perennial or annual **3**
3 Perennial; corolla and calyx blue or purplish ..... ***L. sinuatum***
3 Annual; corolla and calyx golden yellow ..... ***L. bonduellei***
4 Annual; calyx with 5 long, narrow teeth and decurrent nerves (sect. *Schizhymenium*) **5**
4 Perennial; calyx teeth short with no decurrent nerves **6**
5 Corolla purplish; calyx teeth without a hooked tip ..... ***L. avei***
5 Corolla pink; calyx teeth extended by hooked tip ..... ***L. echioides***
6 No rosette of radical leaves at flowering **7**
6 Rosette of radical leaves present at flowering **9**
7 Leaves spatulate-oblanceolate; panicle dichotomous; spikelets grouped at branch extremity; outer bract entirely scarious (sect. *Nephrophyllum* s.l.) ..... ***L. bellidifolium***
7 Leaves ovate-rounded; panicle non-dichotomous; calcariferous tubercles; one-flowered spikelets (sect. *Pruinosum*) **8**

8 Inner bract twice as long as the outer bract; flattened tubercles without papillae ... ***L. alleizettei*** **[ML]**
8 Inner bract 3-4 times longer than the outer bract; tubercles spiked with papillae..... ***L. pruinosum***
9 Numerous sterile stems **10**
9 No or few sterile stems **14**
10 Inflorescences < 22 cm ..... ***L. intricatum*** **[T]**
10 Inflorescences reaching 40-45 cm **11**
11 Leaves green; inflorescences branched in upper part ..... ***L. hipponense*** **[T]**
11 Leaves glaucous; inflorescences branched in basal part **12**
12 Spikes spreading with uniseriate or distichous spikelets; inner and outer bracts with narrow margins ..... ***L. virgatum***
12 Spikes slightly curved with ± lax spikelets; inner and outer bracts with wide margins **13**
13 Leaves with 1 mm-long mucron; angle of inflorescence branches > 40° ..... ***L. xerophilum*** **[T]**
13 Leaves mucronulate; angle of inflorescence branches < 40° ..... ***L. zeugitanum*** **[T]**
14 Leaves < 2 cm **15**
14 Leaves > 2 cm **16**
15 Inflorescences reaching 40 cm; leaf width > 5 mm, without nerve ..... ***L. pescadense*** **[AT]**
15 Inflorescences < 20 cm; leaf width < 5 mm, with 1 nerve ..... ***L. zembrae*** **[T]**
16 Leaves with pinnate nerves (sect. *Limonium*) **17**
16 Leaves with palmate or indistinct nerves **18**
17 Large corymbiform panicle with erect branches; corolla purplish ..... ***L. narbonense***
17 Spreading branches bearing sessile glomerules; corolla blue ..... ***L. boitardii*** **[T]**
18 Inflorescences distichous (sect. *Limonium* subsect. *Densiflorae*) **19**
18 Inflorescences non-distichous **20**
19 Inflorescences > 20 cm; a few sterile stems; corolla violet ..... ***L. densiflorum***
19 Inflorescences generally < 20 cm; no sterile stems; corolla purplish ..... ***L. gougetianum*** **[AT]**
20 Leaves without mucron **21**
20 Leaves mucronate or with an apical tip **25**
21 Inflorescences in dense panicle > 70 cm; leaves with 3-7 nerves ..... ***L. thaenicum*** **[T]**
21 Inflorescences in lax or narrow panicle < 70 cm; leaves with < 3 nerves **22**
22 Leaves green, flat; inflorescence branched from the base ..... ***L. elfahsianum*** **[T]**
22 Leaves glaucous, coriaceous; inflorescence branched at the upper part **23**
23 Leaves glaucous on only one face reaching 12 cm; inner bract with acute apex and 3 times longer than outer bract ..... ***L. spathulatum*** **[M]**
23 Leaves entirely glaucous; inner bract with obtuse apex and 2 times longer than outer bract ... **24**
24 Inflorescences in lax panicle; leaves oblanceolate with apex acute to obtuse; fertile branches < 8 cm; calyx < 5.4 mm; corolla diameter < 6.5 mm ..... ***L. punicum*** **[T]**
24 Inflorescences in narrow panicle; leaves cuneate-spatulate with apex obtuse to rounded; fertile branches < 20 cm; calyx > 5.4 mm; corolla diameter > 7.0 mm ..... ***L. serratum*** **[T]**
25 Leaves < 7 × 1.5 cm **26**
25 Leaves > 7 × 1.5 cm **31**
26 No or rare sterile stems; leaves mucronate or ended by an apical tip **27**
26 Few sterile stems; leaves mucronulate **28**
27 Leaves coriaceous, reddish glaucous, ended by an apical tip > 1 mm, with 1-5 nerves; inflorescences reaching 60 cm, branched in the upper part ..... ***L. cercinense*** **[T]**
27 Leaves flat, glaucous, mucronate, with 1-3(5) nerves; inflorescences < 30 cm, branched in the lower part ..... ***L. formosum*** **[T]**
28 Leaves reddish glaucous, with apex acute **29**
28 Leaves glaucous, with apex obtuse to rounded **30**

29 Inflorescences < 25 cm; fertile branches reaching 4 cm; outer bract with obtuse apex; calyx > 5 mm ..... ***L. clupeanum*** **[T]**
29 Inflorescences reaching 55 cm; fertile branches reaching 10 cm; outer bract with acute apex; calyx < 5 mm ***L. oblanceolatum*** **[T]**
30 Calyx < 5.3 mm; corolla pale reddish violet, diameter < 6 mm ***L. lacertosum*** **[T]**
30 Calyx > 5.3 mm; corolla reddish violet, diameter > 6 mm ***L. pyramidatum*** **[T]**
31 Leaves with indistinct nerves; corolla whitish ***L. tunetanum*** **[ATL]**
31 Leaves with 1-10 nerves; corolla violet **32**
32 Leaves ended by an apical tip > 1 mm **33**
32 Leaves only mucronate or mucronulate **37**
33 Spikes lax > 3 cm, with < 5 spikelets/cm ***L. menigense*** **[T]**
33 Spikes dense < 3 cm, with > 5 spikelets/cm **34**
34 Leaf length < 10 x 2.2 cm, with apex acute ***L. steppicum*** **[T]**
34 Leaf length > 10 cm and/or leaf width > 2.2 cm, with apex obtuse to round **35**
35 Few short, branched sterile stems; leaves < 10 cm ***L. neapolense*** **[T]**
35 Generally no sterile stems; leaves reaching 15-20 cm **36**
36 Spikes rather lax reaching 3-4 cm, with < 6 spikelets/cm . ***L. delicatulum*** subsp. ***orientale*** [**AT**]
36 Spikes dense < 1.5 cm, with > 6 spikelets/cm ***L. byzacium*** **[T]**
37 Leaves with < 3 nerves **38**
37 Leaves with > 3 nerves **40**
38 Spikes > 2 cm; spikelets > 7 mm; calyx > 5.5 mm; corolla diameter > 7.5 mm ....***L. korbousense*** **[T]**
38 Spikes < 2 cm; spikelets < 7 mm; calyx < 5.5 mm; corolla diameter < 7.5 mm **39**
39 Spikelets > 5 mm; corolla diameter > 6 mm ***L. confertum*** **[T]**
39’ Spikelets < 5 mm; corolla diameter < 5 mm ***L. tritonianum*** **[T]**
40 Inflorescences < 50 cm, branched in the lower part; leaves mucronate; spikes with > 8 spikelets/cm ***L. comosum*** **[T]**
40 Inflorescences > 50 cm, branched in the upper part; leaves mucronulate; spikes with < 8 spikelets/cm **41**
41 Leaves reddish glaucous; spikelets < 5 mm ***L. rubescens*** **[ATL]**
41 Leaves glaucous; spikelets > 5 mm **42**
42 Leaves with apex acute, mucronulate; spikes with 4-7 spikelets/cm ***L. kairouanum*** **[T]**
42 Leaves with apex obtuse, mucronate; spikes with 2-5 spikelets/cm ***L. tacapense*** **[T]**

Biogeography and endemism

Notwithstanding its small surface area, Tunisia hosts on its own 43 taxa of *Limonium*. This is the highest diversity recorded in North Africa, compared to Morocco (36), Algeria (28), Libya (17) and Egypt (13) (Dobignard & Chatelain 2010). The distribution of *Limonium* in Tunisia (Electronic Supplementay File1, Fig. S1) reveals that this great diversity results mainly both from the length of the Tunisian coasts in relation to the country’s surface area and the wide range of bioclimates they cover, from the arid Saharan bioclimate to the humid Meso-Mediterranean one.

In addition, the genus *Limonium* is strongly distinguished from the other genera of the flora of Tunisia, being the richest in endemics. Indeed, the overwhelming majority of its taxa are strictly endemic to the country (Domina & El Mokni 2019) (T, 26 taxa, *ca.* 62 %; Fig. 1). This exceptional endemism rate, ranks the country second in North Africa after the Canary Islands (82,6%) (Dobignard & Chatelain 2010). Except for *L. boitardii*, described

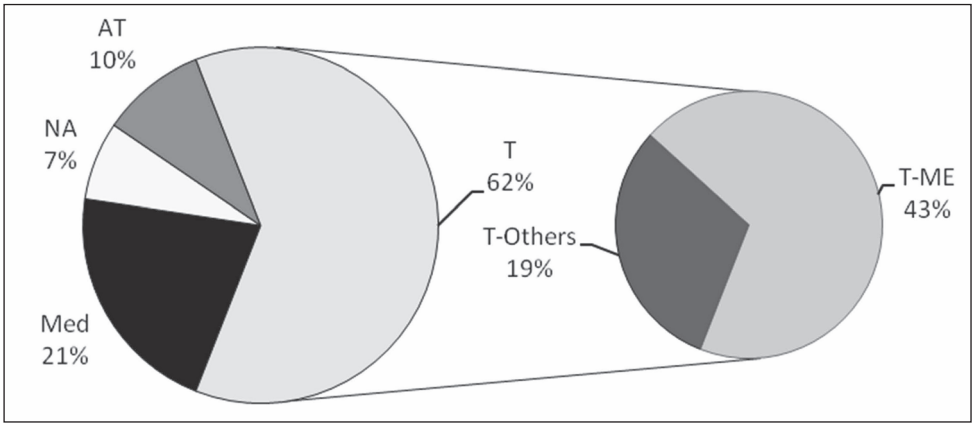

Fig. 1. Chorological spectrum of Tunisian *Limonium* endemic taxa: Tunisian endemics (T), including micro-endemics (T-ME) and other Tunisian endemics (T-Others), Algero-Tunisian endemics (AT), North African endemics (NA) and Mediterranean endemics (Med).

in the 1930s (Maire 1937), all endemic species have been described recently (Pignatti 1982; Brullo & Erben 1989; Erben 2001; Bartolo & al. 2003; Brullo & Giusso del Galdo 2006; Sefi & al. 2020). Among these 26 taxa, 18 are restricted to small geographical areas and present significant conservation issues (ESF1, Fig. S2). Such microendemics (T-ME, ca. 43 %) probably result from long-term apomixis and hybridization events (Palop-Esteban & al. 2007; Brullo & Erben 2016). Considering exclusive endemics and those shared with conterminous countries, the total (T and AT endemics) represents *ca.* 71% of all *Limonium* taxa occurring in Tunisia.

The remaining taxa include 3 North African endemics (including Maghrebi, Algero-Tuniso-Libyan and Maghrebo-Libyan; NA, *ca.* 9 %) and 9 more widely distributed taxa (Med, *ca.* 21 %). The latter include 5 species with a wide Mediterranean range (*L. avei*, *L. echioides*, *L. narbonense*, *L. sinuatum* and *L. virgatum*), one Ibero-North-African species (*L. bonduellei*) and 3 species with particularly interesting distributions: *L. lobatum*, a Mediterranean-Irano-Turanian species, has the largest distribution of the *Limonium* taxa present in Tunisia; *L. bellidifolium* occurs exclusively in southern Europe with the exception of Tunisia (where it is located only in the NE, near Radès and Hammam-Lif; Pottier-Alapetite 1981), suggesting past immigration from Sardinia; and finally, *L. pruinosum* occurs from Syria and Lebanon to Libya and Tunisia, the latter being the western limit of its range.

Insular and peninsular areas are particularly noteworthy, due to the increased speciation process that leads to high levels of endemism (Whittaker & Fernández-Palacios 2007; Kier & al. 2009). Their role as a long-term climatic refuge area has also promoted speciation in the genus *Limonium* within the Mediterranean (Brullo & Erben 2016). Among the Tunisian endemic species of *Limonium*, 7 are strictly endemic to the islands and peninsulas: *L. cercinense* (Kerkennah archipelago), *L. formosum* (Djerba island), *L. lacertosum* (Cap Serrat and Cap Negro peninsulas), *L. steppicum* (Djerba island and Zarzis peninsula), and *L. clupeanum*, *L. korbousense* and *L. zeugitanum* (Cap Bon peninsula). Moreover, 7 others are mainly distributed

on islands and peninsulas, but reach the nearby continental coasts: *L. confertum*, *L. gougetianum*, *L. intricatum*, *L. menigense*, *L. pescadense*, *L. pyramidatum* and *L. zembrae*.

Chorology and ecology

The distribution of *Limonium* taxa according to the Tunisian physiographic subdivisions (ESF1, Fig. S1) highlights their mainly coastal ecology, as well as the richness of the northern coasts. While the Northeast (NE), the Center (C) and the South (S) each harbor 16-17 taxa (*i.e.* 40 % of all *Limonium* taxa in Tunisia), the Cap Bon (CB) and Mogods (Mog) appear to be the richest regions if their relative areas are considered (ESF1, Fig. S1). Besides, it is interesting to emphasize the frequency of occurrences of Mediterranean taxa, characterized in Tunisia by wide distributions, spanning over 4 to 5 geographical regions. These are particularly *L. avei*, *L. echioides* and *L. virgatum*, as well as the Mediterraneo-Irano-Turanian species *L. lobatum* (ESF1, Fig. S3). On the other hand, the analysis of the ecological requirements of Tunisian *Limonium* taxa (Fig. 2) shows a significant preponderance of halophytes (Hal, 79 %) *versus* indifferent taxa (Indif, 5 %) and non-halophytes (NHal, 16 %). Commonly referred to as 'sea lavenders', *Limonium* species indeed occur more frequently in salty habitats, such as salt marshes and sea coasts.

Nonetheless, some taxa stand out markedly, being more or less indifferent to salinity. Firstly, *L. alleizettei* and *L. pruinosum* can develop in both salty and non-salty steppe environments, with however a predilection for gypsum outcrops (Pottier-Alapetite 1981). Secondly, *L. avei*, *L. bonduellei*, *L. echioides*, *L. elfahsanium* and *L. kairouanum* are non-halophilous taxa of arid environments. The two latter are microendemics restricted to a single area, namely the regions of El Fahs (TD) and Kairouan (C) respectively, in matorrals on silty-sandy substrates for the first taxon, and around dry depressions on arid soils for the second one (Brullo & Erben 1989; Brullo & Giusso del Galdo 2006). Finally, two taxa (*L. lobatum* and *L. tacapense*) develop along the banks of wadis in more or less freshwater habitats.

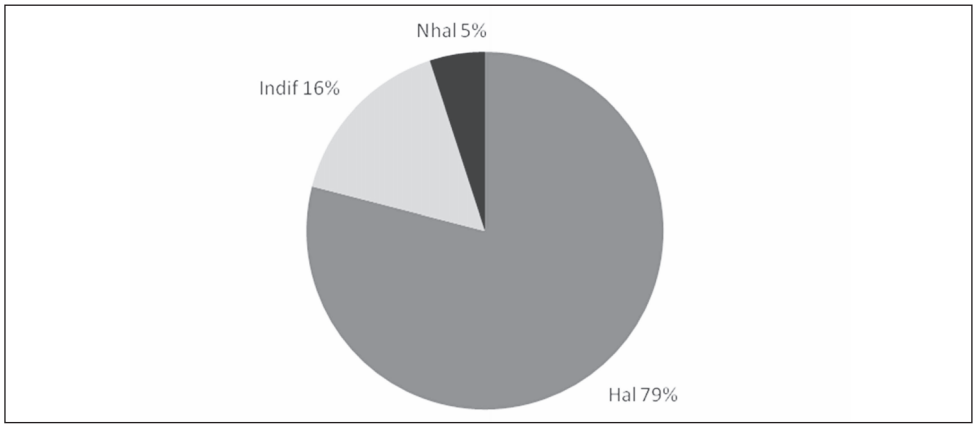

Fig. 2. Ecological spectrum of Tunisian *Limonium*: Halophytes (Hal), Indifferent (Indif), Non-halophytes (Nhal).

The *Limonium* taxa occurring in Tunisia are mainly perennial herbs (hemicryptophytes, 81 %) or dwarf shrubs (chamaephytes, 9 %). The other four species (*L. avei*, *L. bonduellei*, *L. echioides* and *L. lobatum*) are annuals (therophytes, 9 %). The prevalence of perennial taxa (*ca.* 90 %) can be explained by the salinity and aridity that characterize the coastal habitats of most *Limonium* taxa, namely saltmarshes and seashores (Brullo & Erben 2016; Sefi & al. 2020).

Conservation

Assessment

The current state of the art on the Tunisian *Limonium*, supplemented by recent field surveys, has allowed to assess at the regional level 21 % as Least Concern (LC), 5 % as Near Threatened (NT) and 50 % as Threatened, the remaining 24% being classified as Data Deficient (DD) (Fig. 3; ESF1, Table S1). Threatened taxa encompass the following categories: 33 % Vulnerable (VU), 10 % Endangered (EN) and 7 % Critically endangered (CR). During this assessment, the IUCN criteria and thresholds most applied were B1 and B2, related to the geographical distribution as indicators for either extent of occurrence (EOO) and/or area of occupancy (AOO). These criteria led to assess 7 taxa as CR (3) and EN (4). Criterion D was also used to appraise mainly microendemics (13 taxa) with a restricted population, such as *L. kairouanum*, *L. korbousense*, *L. menigense*, *L. neapolense*, *L. punicum*, etc.

Threats

Preferentially growing in coastal regions, the *Limonium* taxa assessed as Threatened (e.g. *L. cercinense*, *L. gougetianum*, *L. hipponense*, *L. intricatum*, etc.), are potentially imperiled by the deterioration of their habitat quality. These habitats, generally with easy

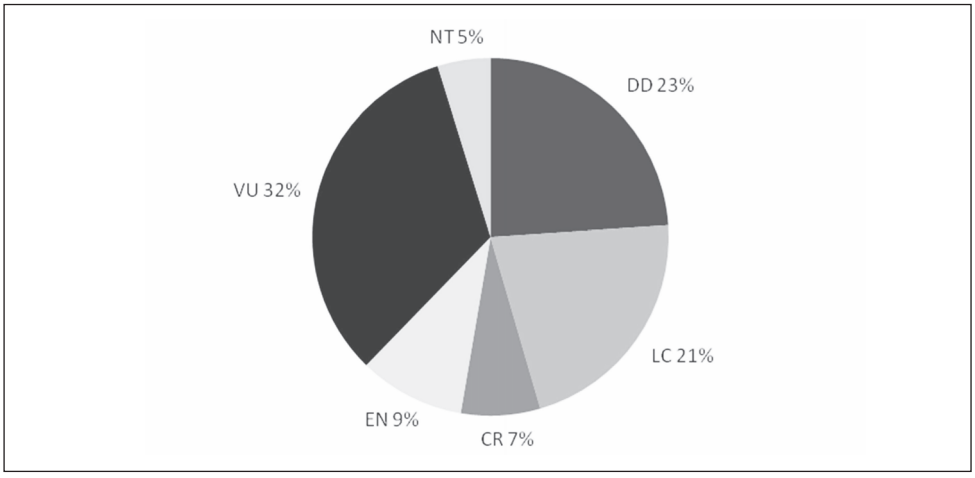

Fig. 3. IUCN Red List categories of *Limonium* occurring in Tunisia: Critically Endangered (CR), Data Deficient (DD), Endangered (EN), Least Concern (LC), Near Threatened (NT) and Vulnerable (VU).

access (coastal fringes, roadsides, urban areas), are severely affected by anthropic disturbances, mainly due to anarchic and illegal urbanization, uncontrolled tourism (recreational activities) and the extension of touristic facilities (Threats 1.1, 1.3, 6.1), leading to a decrease, even a fragmentation and loss of the habitat. The negligence of the inhabitants and users of the sites make them generally polluted and altered by waste of all kinds (Threat 9.4). Overgrazing (Threat 2.3), drought (Threat 11.2) and desertification (Threat 11.1) of steppes (Le Houérou 2001) also threaten some taxa, such as *L. formosum*, *L. kairouanum, L. korbousense* and *L. steppicum*. Such threats, evidenced in Tunisia (Ghrabi-Gammar & al. 2020; Ben Charfi & Numa 2021), have also been reported elsewhere, for instance concerning *L. duriaei* in Algeria and Morocco (Rhazi & Grillas 2010) or *L. strictissimum* in Corsica and Sardinia (de Montmollin & Strahm 2005).

Eleven taxa are included in Key Biodiversity Areas (KBA) and Important Plant Areas (IPA), and of these, 7 are enclosed in protected areas (National Parks and/or Nature Reserves) (Table 2). Some of them, namely *L. gougetianum*, *L. intricatum*, *L. pescadense*, *L. pyramidatum* and *L. zembrae*, grow in rocky habitats, generally difficult to access. These habitats are little threatened (except by drought) and are therefore relatively well preserved, constituting a refuge for these Tunisian microendemics (Pavon & Véla 2011; Véla & Pavon 2012; Greuter & Domina 2015).

Finally, 6 taxa develop in sites included in the Ramsar convention. Nevertheless, it should be brought to mind that the designation of a Ramsar site does not guarantee any particular protection, this being the prerogative of national legislation (Matthews 2013). These 6 taxa together with the remaining 29 ones do not benefit from any conservation action and continue to be heavily impacted by human activities. It is therefore, increasingly urgent to undertake conservation actions in order to abate these threats and to protect fragile habitats, especially when they host microendemic species such as *L. formosum* growing on the island of Djerba.

Djerba 'la douce', the island of Limonium

Djerba, the largest island (30 km long and 20 km wide) on the North African coast, is located in Southeastern Tunisia. It is a mythic island, known as the 'lotophagi island' in Homer's Odyssey (late 8th century BC). The lôtós, which according to Homer is a delicacy so sweet that it made Ulysses' companions forget everything, would be the fruit of the native *Ziziphus lotus* (Ballabriga 1968). This legend could explain the name '*Djerba la douce*' (*i.e.* Djerba the sweet), which also evokes the mildness of the island's climate.

From a scientific point of view, Djerba is a remarkable island area, constituting a 'climatic refuge' favorable to the process of speciation, hence its richness today in microendemics such as *Limonium*. It belongs to the arid Thermo-Mediterranean bioclimatic belt and is characterized by halophilous and gypso-halophilous coastal habitats. It is already endowed with three Ramsar sites, and soon a fourth is being included. Most of the island is a sandy plain rarely exceeding 20 m above sea level, edged by mobile and fixed dunes, lagoons flooded with saltwater, and some outcrops of sandstone and clay-limestone rocks. In addition to its three Ramsar sites, Djerba is classified as a *Key Biodiversity Area* (KBA), *Important Plant Area* (IPA). (Valderrabano & al. 2018). It is home to a rich and diversified vascular flora, estimated to 408 taxa (Vanden Berghen 1981), with 7 Tunisian endemic taxa including 5 *Limonium* species. Recent botanical investigations allowed us to update the

data on the 10 *Limonium* inhabiting the island and to describe an eleventh one, also present on the conterminous Zarzis peninsula (*L. steppicum*; Sefi & al. 2020). Two species (*L. formosum* and *L. menigense*) are strictly endemic to Djerba. According to the available data, *L. menigense* is considered as endangered (EN). Nevertheless, it was not found again during our recent fieldworks, and is therefore possibly extinct. Historical locations need to be tracked accurately to verify if the species still exists.

The microendemic species of *Limonium* are mostly enfeoffed to coastal wetlands and dunes. The inclusion of these habitats in the Ramsar list and their belonging to the Maritime Public Domain provides them with some theoretical protection (prohibited construction), but illegal urbanism, uncontrolled touristic activities and the resulting pollution represent high threats, especially for the fragile habitat of *L. formosum*. This species is restricted to a small sandy and rocky coastal area confined between two hotels and threatened by a project for the construction of a seaside tourist attraction. An *ex-situ* multiplication trial was set up, in order to reintroduce it into other similar habitats on the island; training sessions were conducted for associations active in the protection of biodiversity to monitor population and habitat trends of this taxon.

An initiative to create a natural micro-reserve for the *in-situ* protection of the island's microendemic was developed. It has only resulted in the elaboration and adoption of a participatory action plan for its protection by the representatives of different structures (*Agence de Protection et d'Aménagement du Littoral*, *Direction Générale des Forêts*, municipality, tourism office, local associations), which intervene on the site at regional and national levels. Nevertheless, this is not enough to guarantee the protection of the species. For a concrete and effective protection, this participatory plan must necessarily be imple-

Table 2. Tunisian *Limonium* taxa occurring in Ramsar sites (RS), National Parks (NP), National Reserves (NR), Key Biodiversity Areas (KBA) and Important Plant Areas (IPA).

Taxon	RS	Protected Areas	KBA	IPA
L. boitardii		NP - NR	x	x
L. cercinense	x		x	x
L. confertum	x			
L. formosum			x	x
L. gougetianum		NR	x	x
L. intricatum		NR	x	x
L. menigense	x		x	x
L. pescadense		NP - NR	x	x
L. pyramidatum		NR	x	x
L. sinuatum		NP	x	x
L. steppicum	x		x	x
L. thaenicum	x			
L. zembrae		NP - NR	x	x
L. zeugitanum	x			

mented and followed by the creation in the near future of a micro-reserve. The active involvement of all stakeholders, including the local community, is a guarantee of sustainable protection of this microendemic of the island, especially from the urbanization project that threatens its only habitat.

Conclusion

While being the smallest country in North Africa, Tunisia hosts the highest diversity in *Limonium* taxa. This may be related to the north-south orientation of the coasts that span from the arid Saharan to the humid Meso-Mediterranean bioclimate. The only other country with a comparable geography is Morocco, which has almost as many taxa as Tunisia (Dobignard & Chatelain 2013). The main differences between the two countries that could explain the greater richness of Tunisia are probably the physiography of their southern steppe regions, which are occupied by vast sandy and rocky plains dotted with salt lakes (chotts) and only small reliefs (jbels) in Tunisia (Le Houérou 1959), while they are much more mountainous and devoid of chotts in Morocco, as well as the location of Tunisia, at the crossroads between the biogeographical influences of the Sahara, the Tyrrhenian region and the western and eastern basins of the Mediterranean. Nevertheless, the number of recent discoveries in Tunisia suggests that meticulous survey work in other North African countries would lead to a probable increase in the number of *Limonium* species.

This second synthesis for Tunisia after that of Brullo & Erben (1989), is therefore only a first step towards the knowledge of the genus *Limonium* in North Africa. Our analysis of the different features related to biogeography, endemism, chorology and ecology corroborates previous studies carried out in the Mediterranean (Pignatti 1962; Brullo 1978, 1980; Artelari 1984; Brullo & Erben 1989, 2016; Arrigoni & Diana Corrias 1993, 1999), as to the complexity of the genus *Limonium* and to the preponderant role that geographical and ecological isolation plays in its diversity and speciation.

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