



# New occurrences for the flora of Lebanon: *Sideritis syriaca* subsp. *nusairiensis* (Post) Hub.-Mor. (Lamiaceae) and *Thymus sipyleus* Boiss. (Lamiaceae) and consideration on their distribution, natural habitats, and conservation status

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## Abstract

Investigations carried out during 2019 on the vascular flora of Jabal Akroum, the northernmost part of the Mount Lebanon range near the Syrian border, yielded two new records of Lamiaceae species for the flora of Lebanon: *Sideritis syriaca* subsp. *nusairiensis* (Post) Hub.-Mor. and *Thymus sipyleus* Boiss. We present findings on the distribution and ecology of these species as well as their conservation status at the national level in accordance with International Union for the Conservation of Nature guidelines. We also report on the natural habitats of Jabal Akroum.

## Keywords

Akkar, endemism, Lamiaceae, Red List, northeastern Mediterranean

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## Introduction

*Sideritis* L. is a Western Palearctic genus of Lamiaceae that includes 193 perennial and annual species distributed in the Mediterranean, the Canary Islands, and Madeira (González-Burgos et al. 2011; Dülgeroğlu 2017). Seven taxa of *Sideritis* have been recorded from Lebanon (Post and Dinsmore 1932; Mouterde 1984; Tohme 2014): *Sideritis balansae* Boiss., *Sideritis curvidens* Stapf, *Sideritis libanotica* Labill., *Sideritis montana* subsp. *montana* L., *Sideritis montana* subsp. *remota* (d'Urv.) P. W. Ball, *Sideritis perfoliata* L., and *Sideritis pullulans* Vent.

*Sideritis syriaca* L. belongs to *Sideritis* sect. *Empedoclia* (Rafin.) Benthham which includes two taxa, *S. syri-*

*aca* subsp. *syriaca* and *S. syriaca* subsp. *nusairiensis* (Post) Hub.-Mor. Both these subspecies are endemic to the northeastern Mediterranean, mainly Turkey (Esra et al. 2009). There have been some discussions about the taxonomy of *S. syriaca* in the past. In Flora Europaea (Tutin et al. 1972), *S. syriaca sensus lato* included *Sideritis cretica* Boiss. (not *Sideritis cretica* L.), *S. raeseri* Boiss. et Heldr., *S. sicula* Ucria, and *S. taurica* Stephan ex Willd., whereas other taxonomists considered these taxa as separate species (Davis et al. 1965). *Sideritis syriaca* subsp. *syriaca* has recently been considered as exclusively endemic to Crete (Euro+Med 2019; WCSP 2020).

Only the taxonomy of Bulgarian subpopulations remains uncertain. Recent chemotaxonomic and morphometric studies have proven that Bulgarian *S. syriaca* is closer to Turkish *S. taurica* and suggest further verification of the taxonomic status of the Balkan subpopulations (Stanova et al. 2015; Aneva et al. 2019).

Previously known as *Sideritis nusairiensis* Post, *S. syriaca* subsp. *nusairiensis* was described based on an 1890 collection of Georges Post in Masyaf (Qalaat el-Musyaf) in the western mountains of Syria (historically called Nusayriyah Mountains or Jibal al-Ansariya) (Post and Dinsmore 1932; Davis et al. 1965). The taxon is currently considered to be endemic to Turkey and Syria. In Turkey, it is distributed in the Nur Mountains (historically known as Amanus) and Jabal Aqra (historically called Mount Casius, Kiliç Dagi in Turkish). In Syria, the taxon only occurs in the western mountain range and was collected several times in Slenfe, Nabi Mata (above Slenfe), Jaoubat Bourghal, and Masyaf.

One of the eight richest genera of the Lamiaceae, *Thymus* L. is a Western Palearctic genus that includes around 215 species distributed across Greenland, Europe, the Mediterranean, East Africa, the Himalayas, and Siberia (Morales 1997). Two species of *Thymus* have been recorded in Lebanon: *Thymus hirsutus* Bieb. and *T. syriacus* Boiss. (Mouterde 1984; Tohme 2014). *Thymus sipyleus* Boiss. is included in *T.* sect. *Hyphodromi* subsect. *Thymbropsis* Jalas ex R. Morales (Morales 1997). It was described in *Diagnoses Plantarum Orientalium novarum* from the holotype, which was collected in Mount Sipylus (Spil Dağı) in Manisa province in Turkey's Aegean Region (Boissier 1844; Davis 1965). The species is distributed in the Greek East Aegean Islands, Turkey, and the countries of the Caucasus, namely Georgia, Armenia, Azerbaijan, and North Ossetia-Alania (Euro+Med 2019; GBIF 2019). The southernmost edge of the range of *T. sipyleus* was historically Mount Casius (Davis et al. 1965; Mouterde 1984).

As a result of its unique position in the Levant, its complex topography and rugged mountainous terrain (Khawlie et al. 2002), Mount Lebanon constitutes a mosaic of natural habitats sheltering a significantly high biodiversity (Talhok et al. 2018). Impacted by intense human activities and important demography, Mount Lebanon, Anti-Lebanon, and the neighbouring Levantine regions are nevertheless biodiversity hotspots of the Mediterranean Basin, but also among the most threatened (Medail et al. 1997). Recent studies on important plant areas (IPAs) (Bou Dagher-Kharrat et al. 2018) and key biodiversity areas (KBA) (Valderrábano et al. 2018) highlighted the importance of the northern region of the Governorate of Akkar for its considerable floristic richness and high rate of endemism. Identified as an IPA and a KBA, this region includes the watersheds of Nahr el-Kebir, Wadi Khaled, and Jabal Akroum.

The river Nahr el-Kebir marks a natural border between Lebanon and Syria where regional tensions discourage exhaustive visits to this securitized area (Hutson

2011; Mouawad 2018). Geologically unique due to its basaltic bedrock, Nahr el-Kebir is situated at the northern end of the ridges of Mount Lebanon (Akkermans 2003) where it makes a boundary between the mountainous Akkar region and the plain of Homs in Syria. Often referred to as the Homs/Akkar Gap, this area is known to host very restricted endemic plant species, namely *Vicia hyaeniscyamus* Mt. (Fabaceae) and *Lathyrus basalticus* Rech.f. (Fabaceae) (Mouterde 1984). A recent study also reported the discovery of a new highly restricted endemic species in the area, *Isoetes libanotica* Musselman, Bolin & R.D.Bray (Isoetaceae), which highlights how little is known about the local flora (Bolin et al. 2011). The nearby mountain of Jabal Akroum constitutes the northernmost mountain of the Mount Lebanon range. Located immediately westward of Nahr el-Kebir, Jabal Akroum is the final mountain before the Mount Lebanon range descends into the Homs/Akkar gap (Fig. 1). Jabal Akroum remains largely underexplored by biologists. *Sideritis syriaca* subsp. *nusairiensis* (Post) Hub.-Mor. (Lamiaceae) and *Thymus sipyleus* Boiss. (Lamiaceae) were found there.

## Methods

In November 2019 and August 2020, six days and one day of fieldwork, respectively, were carried out for investigation on the floristic diversity and associated natural habitats of Jabal Akroum (Appendix). This mountain rises between 300 to 1260 m in altitude and is oriented north-south with bedrock composed of limestone. The geographic coordinates of the species were recorded in the field. We used Mouterde (1984) as a reference for species identification and distribution, as well as the floras of Syria (Post and Dinsmore 1932), Turkey (Davis et al. 1965), and Europe (Tutin et al. 1972). Familial classification and synonyms were updated in accordance with the information sourced from the International Plant Names Index, the World Checklist of Selected Plant Families (INPI and WCSP 2020), and the Euro-Mediterranean plant diversity which integrates data from Flora Europaea, Med-Checklist, Flora of Macaronesia and from regional and national floras and checklists from the area as well as additional taxonomic and floristic literature (Euro+Med 2019). We prepared the maps using QGIS software (QGIS.org 2020) using layers available from DIVA-GIS (2017) website. The area for each identified habitat and percentage of area covered was drawn and calculated using QGIS. The assessments for both species were made following the guidelines of the International Union for Conservation of Nature (IUCN) Red List categories and criteria (IUCN Standards and Petitions Committee 2019). The collected specimens were given to the Post Herbarium located in the American University of Beirut (BEI).

## Results

### *Sideritis syriaca* subsp. *nusairiensis* (Post) Hub.-

**Mor.**, Bauhinia 6: 291. 1978 (Post 1932; Huber-Morath 1978)

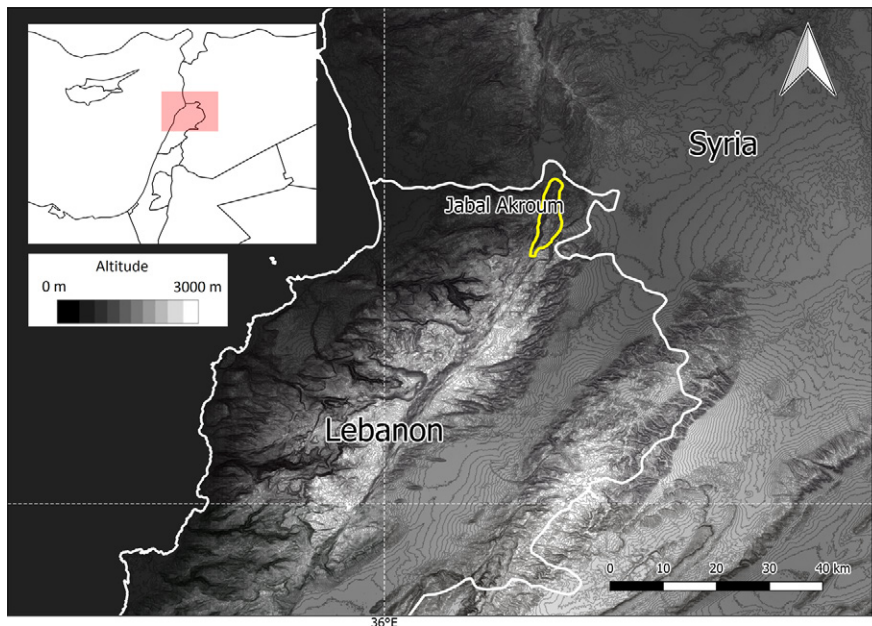
Figures 2–4

**New record.** LEBANON • Akkar, Jabal Akroum; 34.5208°N, 036.3102°E; 1300 m elev.; 14-xi-2019; fl.; H. El Zein (BEI-HELB-403).

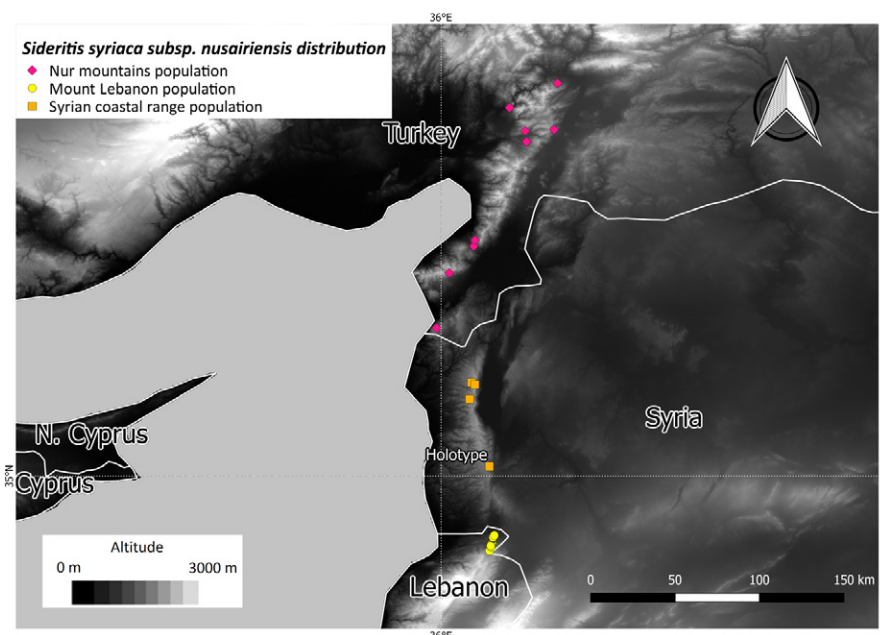
**Phenology.** The flowering period extends from summer to the early fall. Due to warm weather throughout November 2019, some individuals were flowering which allowed for accurate species identification.

**Identification.** *Sideritis syriaca* subsp. *nusairiensis* is a shrub reaching 20 to 80 cm in height. Woolly plant, white tomentose eglandular indumentum. **Leaves** 1–2 × 3–6 cm, basal and low leaves ovate with spatulate petiole, fine or indistinctly crenate-denticulate, cauline leaves sessile, obovate to oblong. **Inflorescence** 3–8 verticillaters, 6-flowered; middle bracts orbicular, 0.6–1 cm, mucronate (mucro 1–5 mm); **Calyx** 7.5–9 mm long, densely white-tomentose, teeth triangular-lanceolate, 2.0–2.5 mm, acute. **Corolla** yellow, 8–11 mm long, hairy and with burgundy ribs inside.

**Habitats.** The species was observed in 28 different quadrats and a total of 337 individuals sparsely scattered were counted along the crest over 10 km (Table 1), occurring

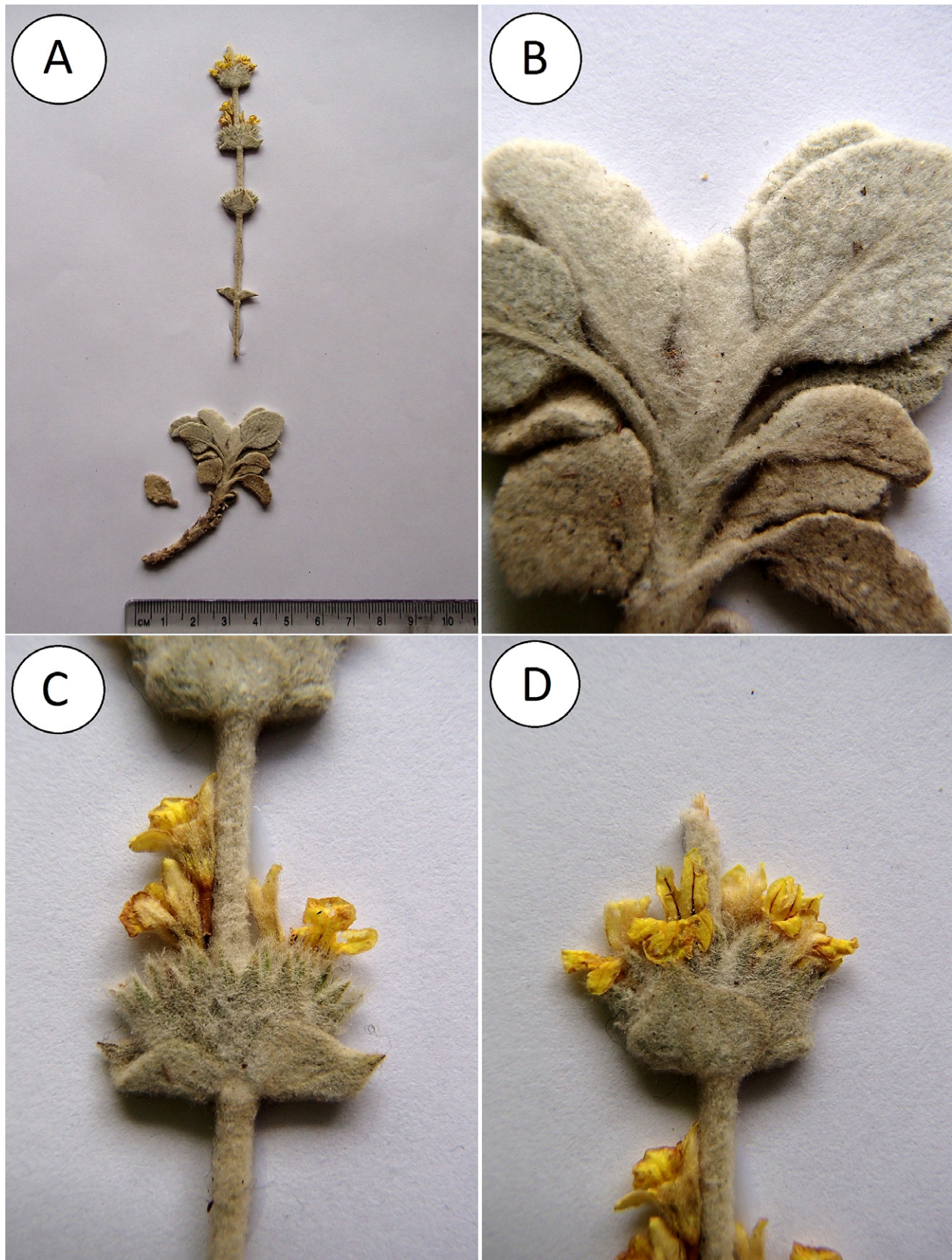


**Figure 1.** Geographical situation of Jabal Akroum in Mount Lebanon.



**Figure 2.** Distribution map of *Sideritis syriaca* subsp. *nusairiensis* (Post) Hub.-Mor. highlighting the records known prior to this work (Post and Dinsmore 1932; Davis et al. 1965; Mouterde 1984) and the occurrences newly reported here.





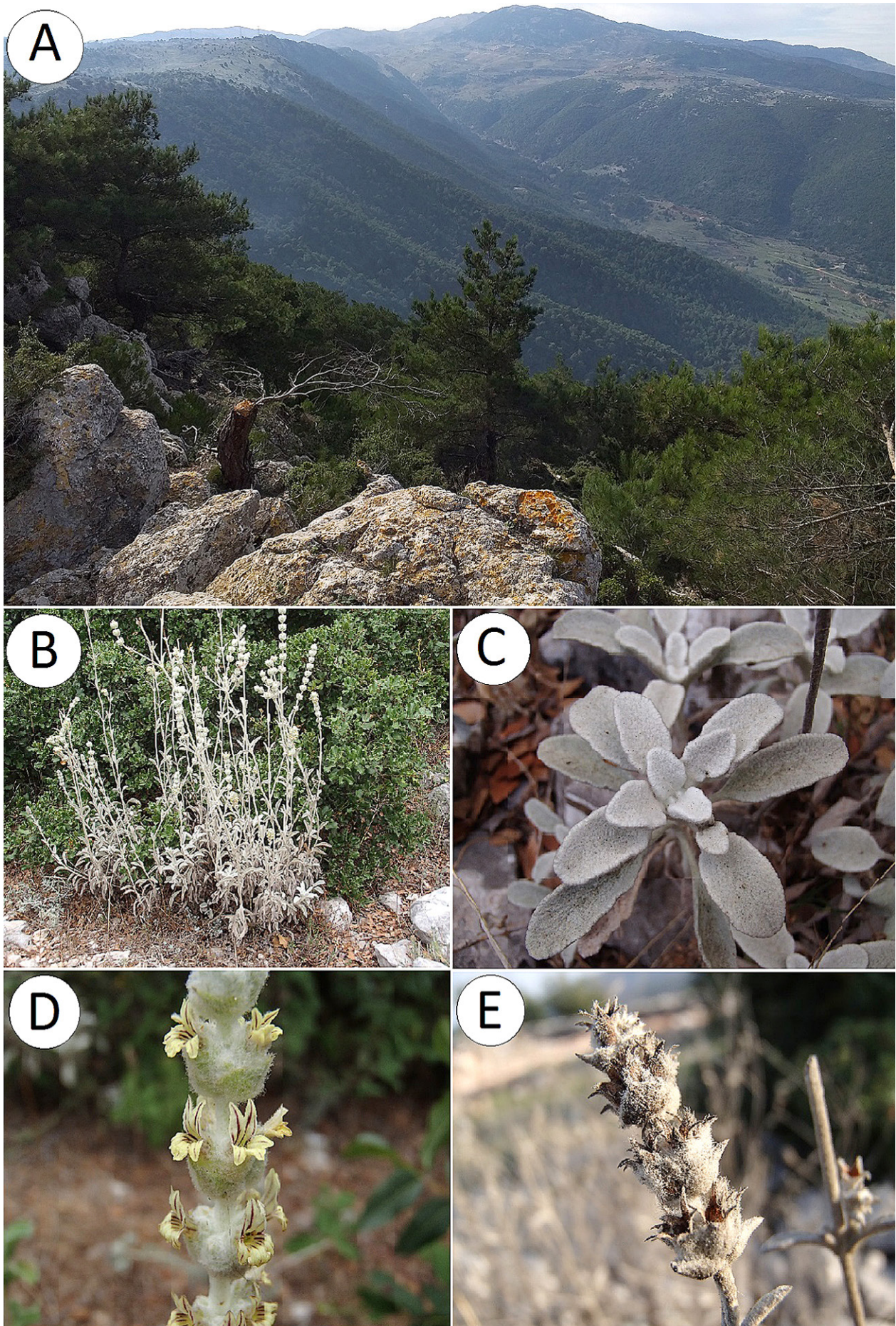
**Figure 3.** *Sideritis syriaca* subsp. *nusairiensis* **A.** Specimen collected in November 2019 on Jabal Akroum (BEI-HELB-403). **B.** Leaves. **C, D.** Inflorescence. Photographs by HE.

in open areas on rocky limestone substrates in different types of habitat. Around 87% of the observed individuals occurred in three habitats: phrygana (43.50%), oak garrigue (29.25%) and oak matorral (14.25%). The rest of

the individuals were distributed between juniper woodlands, pine woodlands and matorrals, oak woodlands and grasslands (Fig. 5).

**Conservation status.** Nationally assessed as Critically





**Figure 4.** *Sideritis syriaca* subsp. *nusairiensis* **A.** Habitat: Rocky limestone crests and edges of pine forest in November 2019 on Jabal Akroum. **B.** General view. **C.** Leaves. **D.** Inflorescence. **E.** Fruits. Photographs taken in November 2019 and August 2020 by HE.



**Table 1.** Geographic coordinates in decimal degrees (WGS84) of the individuals of *Sideritis syriaca* subsp. *nusairiensis* (Post) Hub.-Mor. observed on Jabal Akroum in November 2019 and the types of habitat in which they were observed.

Latitude	Longitude	Verbatim elevation (m)	Individual count	Habitat
34.5208	036.3102	1305	10	<i>Juniperus excelsa</i> arborescent matorral
34.5441	036.3216	1175	5	Kermes oak woodland
34.5454	036.3205	1162	4	<i>Juniperus excelsa</i> arborescent matorral
34.5518	036.3190	1052	1	Eastern kermes oak garrigues
34.5523	036.3180	1033	5	<i>Pinus brutia</i> forests
34.5534	036.3180	1009	3	<i>Pinus brutia</i> forests
34.5552	036.3181	1017	5	Eastern kermes oak garrigues
34.5580	036.3193	1045	7	Eastern kermes oak garrigues
34.5606	036.3202	1030	6	Evergreen oak arborescent matorral
34.5696	036.3236	1014	5	Mediterranean tall-grass
34.5713	036.3268	1105	1	Eastern kermes oak garrigues
34.5742	036.3280	1079	10	Eastern kermes oak garrigues
34.5746	036.3303	1052	2	Evergreen oak arborescent matorral
34.5749	036.3277	1059	15	Evergreen oak arborescent matorral
34.5753	036.3271	968	15	Eastern kermes oak garrigues
34.5792	036.3270	956	25	Eastern kermes oak garrigues
34.5806	036.3278	962	10	Eastern kermes oak garrigues
34.5828	036.3281	941	25	Eastern kermes oak garrigues
34.5852	036.3301	937	25	Evergreen oak arborescent matorral
34.5965	036.3315	813	3	Phrygana
34.6006	036.3320	825	3	Phrygana
34.6040	036.3325	841	40	Phrygana
34.6052	036.3328	808	25	Phrygana
34.6064	036.3320	785	35	Phrygana
34.6072	036.3326	791	6	<i>Pinus brutia</i> arborescent matorral
34.6080	036.3328	782	36	Phrygana
34.6083	036.3320	770	6	<i>Pinus brutia</i> arborescent matorral
34.6208	036.3409	727	5	Phrygana

Endangered, Blab(iii), in Lebanon (Supplementary File 1: IUCN Red List Assessment); globally assessed as being of Least Concern.

*Thymus sipyleus* Boiss., Diagn. Pl. Orient. 5: 16. (Boissier 1844)

Figures 6–8

**New record.** LEBANON • Akkar, Jabal Akroum; 34.5580°N, 036.3193°E; 1045 m elev.; 14-viii-2020; fl.; H. El Zein (BEI-HELB-493).

**Phenology.** The flowering period extends from June to August.

**Identification.** Several individuals of *Thymus sipyleus* were observed (Table 2). Cespituous, low, woody, branching, creeping subshrub forming dense cushions, 10–20 cm in height. **Leaves** 3–4 mm long, ovate, sparsely visible at the base, tightly imbricate decussate, with a few oil dots. **Inflorescence** a compact head with floral bracts similar to leaves and 2-flowered verticillasters. **Calyx.** 3.0–3.8 mm, with equal lips equaling the tube, calyx throat strongly bearded. **Corolla** pink. Due to intense grazing, the plants formed very low patches on the rocky ground.

**Habitats.** Individuals were sparsely scattered along the crest of Jabal Akroum over 3 km. They were always

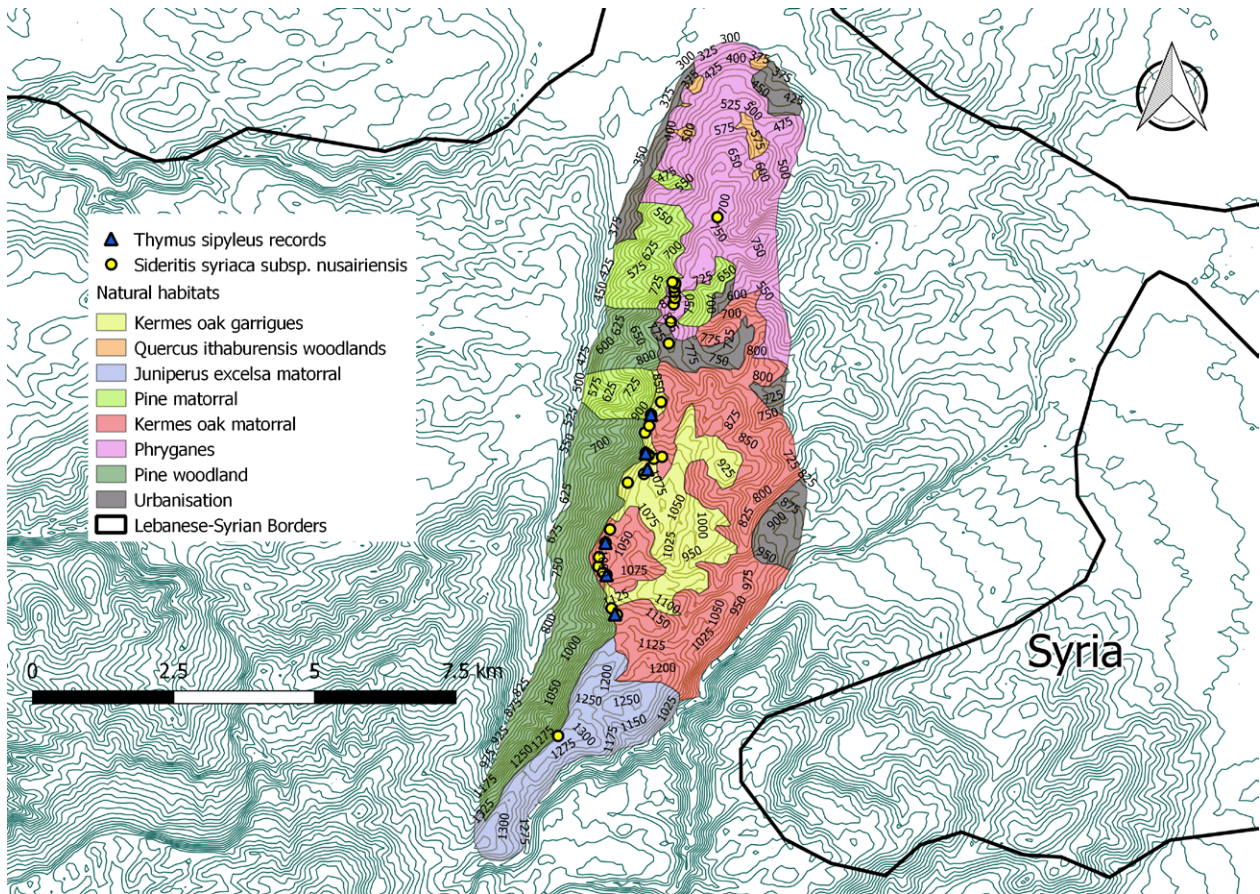
observed in open areas on rocky limestone substrates in different types of habitat between 943 and 1170 m of altitude (Table 2). Three hundred individuals of *Thymus sipyleus* were observed in kermes oak garrigues located on the crest. In this area, grazing had been more intense and was still ongoing. Many flocks were encountered there even though November is beyond the traditional summer grazing season. Other scattered individuals were found further South in oak arborescent matorrals (Fig. 5). This habitat was relatively well preserved and spared from wood cutting and grazing.

**Conservation status.** Nationally assessed as Critically Endangered, Blab(iii), in Lebanon (Supplementary File 2: IUCN Red List Assessment); globally assessed as being of Least Concern.

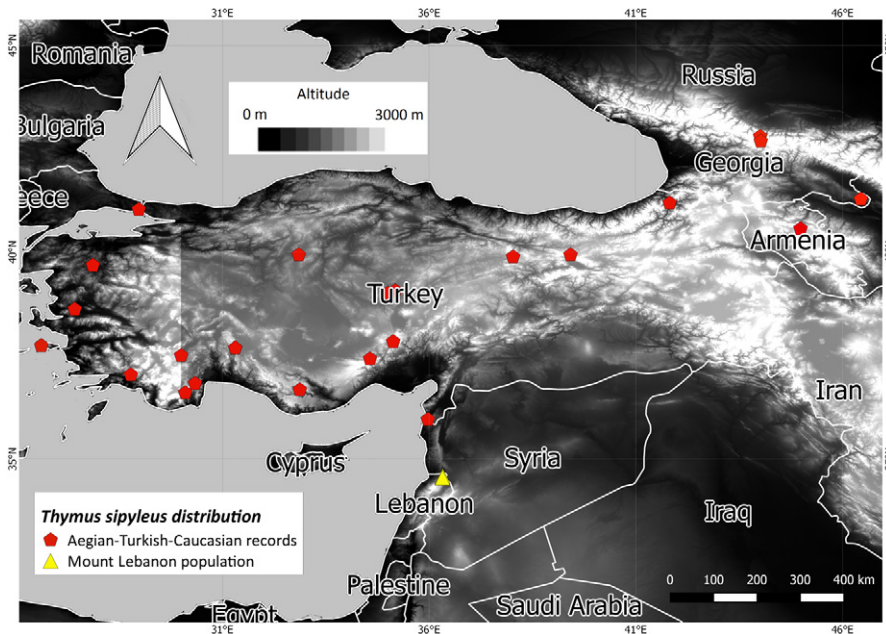
## Discussion

Although never reported in Lebanon, *Sideritis syriaca* subsp. *nusairiensis* is an Eastern Mediterranean element (Davis et al. 1965) endemic to Turkey and Syria. Its nativeness to the area is suggested by its phytogeography, as the species has a similar pattern of distribution to that which is common among Eastern Mediterranean species endemic to the Levantine Mountains. It is distributed between the Nur Mountains, the Jabal Aqra, and the Syrian coastal mountains. The region of Kahramanmaras, the meeting point between Nur Mountains and the Eastern Taurus range, constitutes the northernmost edge of its range. The last known southernmost edge of distribution was Masyaf, which is located only 22 km away from the closest point on Jabal Akroum. Moreover, the Syrian and Turkish subpopulations share the same habitat and ecology (Davis et al. 1965; Mouterde 1984), namely rocky habitats on limestone bedrock. The presence of the species in remote and extreme habitats on the crest all along the Jabal Akroum dismisses the possibility for human introduction. Other plant species endemic to the Levant have the same pattern of distribution. This is the case of *Sideritis libanotica*, also a perennial mountain species of the same genus, which occurs in Mount Lebanon, Anti-Lebanon (including Mount Hermon), the Syrian coastal range, and Jabal Aqra (Davis et al. 1965; Mouterde 1984; Euro+Med 2019). Therefore, it can be considered that *Sideritis syriaca* subsp. *nusairiensis* is native to Jabal Akroum but has not been previously collected.

*Thymus sipyleus* is also an Eastern Mediterranean element (Davis et al. 1965) but with a broader distribution than *Sideritis syriaca* subsp. *nusairiensis* and occurs from western Turkey to the Caucasus. The nativeness of this species is also possible as suggested by phytogeographical argument. *Thymus sipyleus* has a pattern of distribution typical of some species endemic to the Eastern Mediterranean region and the Caucasus. It is distributed from the mountains of the Greek East Aegean Islands and Turkey to the Caucasus. However, there is a disjunction of distribution between Jabal Aqra, the last known southernmost edge of distribution, and Jabal



**Figure 5.** Map of the new records of *Sideritis syriaca* subsp. *nusairiensis* (Post) Hub.-Mor. and *Thymus sipyleus* Boiss. observed on Jabal Akroum in November 2019 and their distribution among the types of habitats

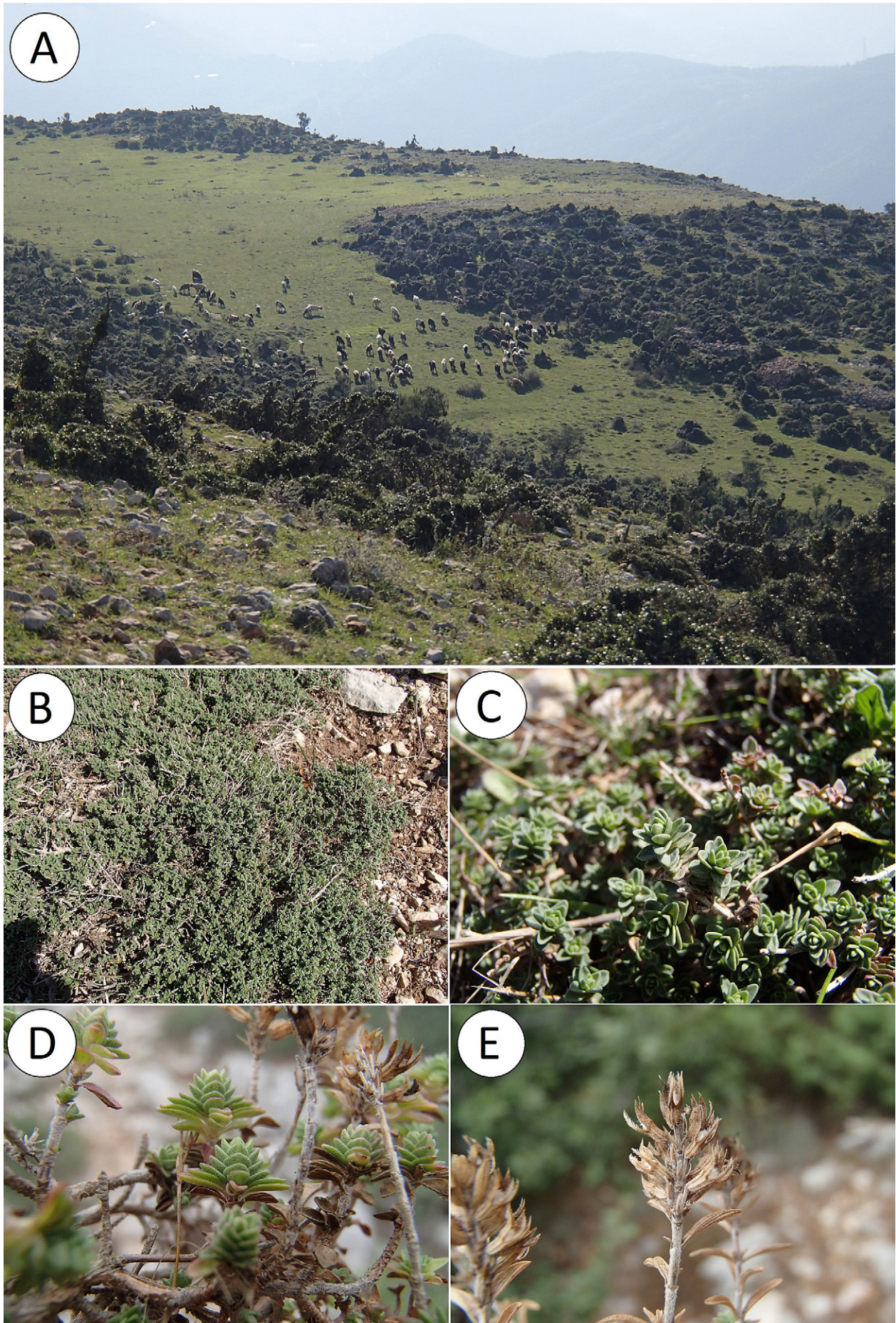


**Figure 6.** Distribution map of *Thymus sipyleus* Boiss. highlighting the records known prior to this work (Post and Dinsmore 1932; Davis et al. 1965; Mouterde 1984) and the occurrences newly reported here.

Akroum, the new southernmost edge. The species was never reported in the Syrian Coastal range, but it could potentially occur within it due to the geographic position of its range and the existence of the same natural habitats as the ones observed in Jabal Akroum. The Greek and

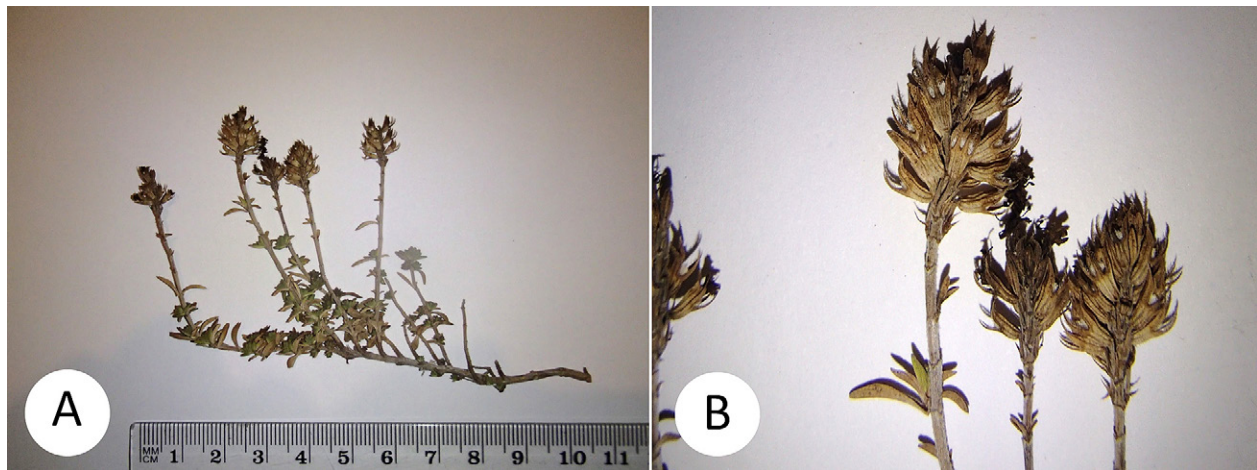
Turkish subpopulations also thrive in rocky habitats on limestone bedrock (Mouterde 1984). Additionally, other species of the genus *Thymus* have a similar distribution, such as *T. hirsutus*, which is extant from the Greek mountains and Turkey to the Nur mountains, the Syrian





**Figure 7.** *Thymus sipyleus* Boiss. **A.** Habitat: oak arborescent matorral with flock of goats in November 2019 on Jabal Akroum. **B.** General view. **C, D.** Leaves. **E.** Fruits. Photographs taken in November 2019 and August 2020 by HE.





**Figure 8.** *Thymus sipyleus* **A.** Specimen collected in August 2020 on Jabal Akroum (BEI-HELB-493). **B.** Inflorescence. Photographs by HE.

**Table 2.** Geographic coordinates in decimal degrees of the individuals of *Thymus sipyleus* Boiss. observed on Jabal Akroum in November 2019 and the types of habitat in which they were observed.

Latitude	Longitude	Verbatim elevation (m)	Individual count	Habitat
34.5442	36.3212	1170	2	<i>Pinus brutia</i> forests
34.5518	36.3195	1051	1	Evergreen oak arborescent matorral
34.5580	36.3193	1045	300	Evergreen oak arborescent matorral
34.5722	36.3274	1065	1	Eastern kermes oak garrigues
34.5753	36.3271	968	1	Eastern kermes oak garrigues
34.5828	36.3281	943	1	Eastern kermes oak garrigues

coastal range, and Mount Lebanon (Davis et al. 1965; Mouterde 1984; POWO 2020). Lastly, the presence of the species in remote and extreme habitats on the crest of Jabal Akroum dismisses the possibility of human introduction. It can therefore be considered that the species is native to Jabal Akroum but has not previously been identified.

The discovery in Jabal Akroum of two plant species endemic to the Eastern Mediterranean region highlights the need for further investigation on the native flora in Mount Lebanon, especially in understudied regions such as the North of the mountain range located in the district of Akkar. The distribution patterns of both species are common for endemic vascular plants of the Eastern Mediterranean and the Levant and it is here proposed that *S. syriaca* subsp. *nusairiensis* and *T. sipyleus* are native to Mount Lebanon and have not been reported due to gaps in knowledge about the local flora. These records constitute the new southernmost edges of the ranges for both species. Not only do these findings increase the number of recognized taxa of *Sideritis* and *Thymus* in the Lebanese flora, but they are also of phytogeographical importance for understanding the affinities between the flora of the Mount Lebanon range, the Syrian coastal range, the Nur mountain range, and the Taurus range. Molecular phylogeographic studies could make a valuable contribution to understanding the lineage of *T. sipyleus* and of the different taxa of *S. syriaca* in the Eastern Mediterranean. Regarding the threat of over-grazing that is

affecting Jabal Akroum in Lebanon, both species were considered as Critically Endangered in Lebanon. Jabal Akroum is the sole locality in which these species occur in Lebanon, and it is therefore the most important site for the preservation of these species.

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## Authors' Contributions

HE and AP carried out the fieldwork. HE collected the specimens, photographed and identified the species, made the distribution maps, and wrote the text. AP revised the text as a native English speaker. We thank the subject editor, Luana Calazans, the editor, Robert Forsyth, and the anonymous reviewers for their helpful comments on the manuscript.

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## Supplemental Data

**Supplemental File 1.** National Red List Assessment of *Sideritis syriaca* subsp. *nusairiensis* (Post) Hub.-Mor.

**Supplemental File 2.** National Red List Assessment of *Thymus sipyleus* Boiss.

## Appendix

**Habitats of Jabal Akroum.** Most of Jabal Akroum was explored, including the crest which has a length of approximately 20 km. The west-oriented slopes of Jabal Akroum are characterised by a dense pine forest located in the municipality of Andqet. This forest is characterised by its good state of conservation as constructions are absent from the western slopes. It constitutes one of the largest forests of *Pinus brutia* in Lebanon. Only two roads cross through the slopes, leading to the other side of the mountain. The east-oriented slopes of Jabal Akroum, less steep, are impacted by human activities and urbanization. Woodlands are sparse and natural habitats are fragmented by roads and many constructions. Ten villages are found on this side of the mountain, including the village of Akroum. The crest is only partly preserved and mostly deforested, over-grazed and exhibits sparsely vegetated areas of garrigues with rocky outcrops in many places. The bedrock is composed of limestone.

Eight types of natural habitats (Figs. 5, A1) were identified on Jabal Akroum during the survey (EUNIS (2012) habitat code in brackets). *Pinus brutia* pine woodlands (G3.75) covered 17% of the area and were spotted exclusively on the western slopes of Jabal Akroum. *Pinus brutia* arborescent matorral (F5.144) covered more than 8% of the area and was spotted on the upper western slopes as transitional habitat between the pine forest and the crest or as a degraded stage of the pine woodlands. *Quercus coccifera* (locally known as *Quercus*



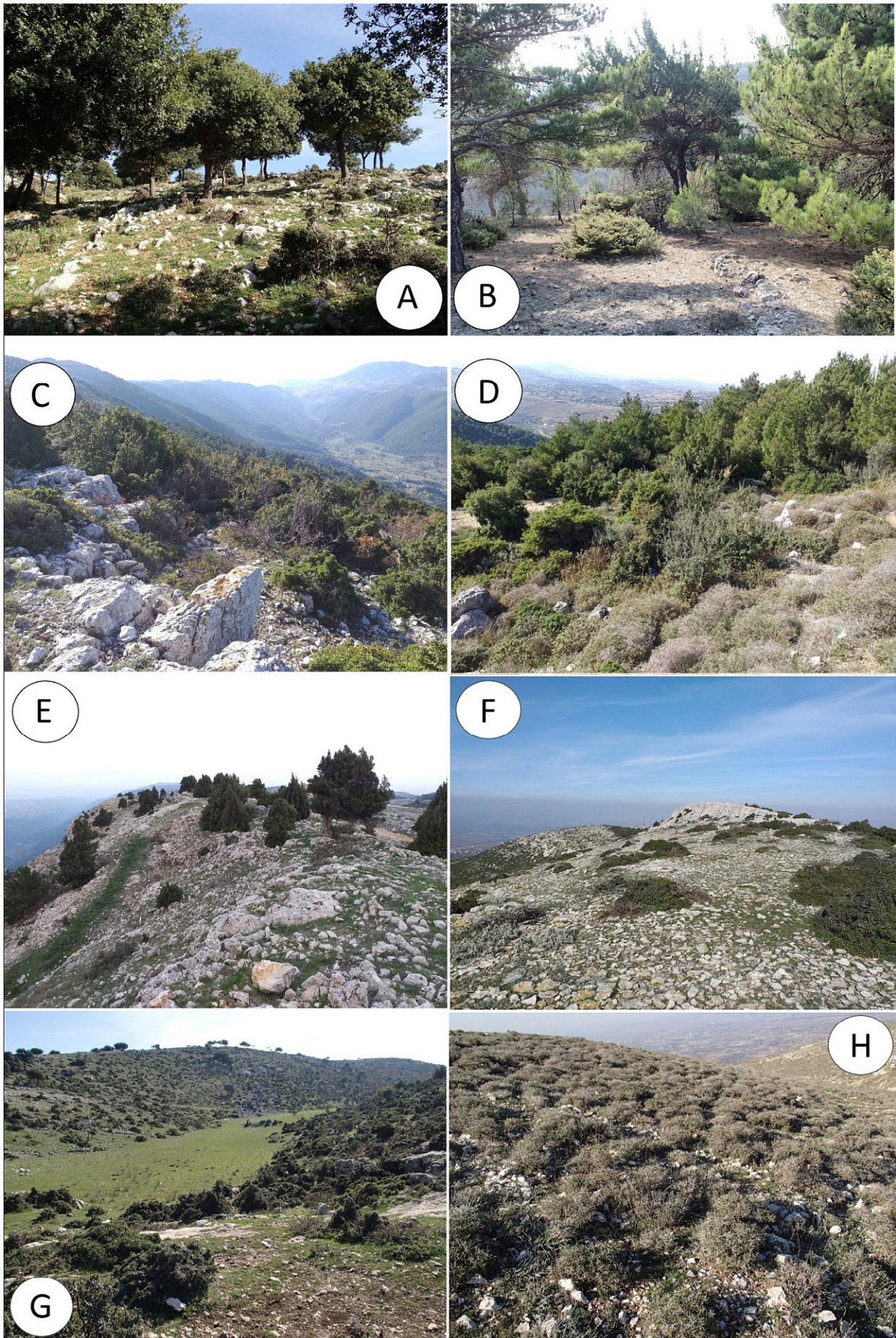
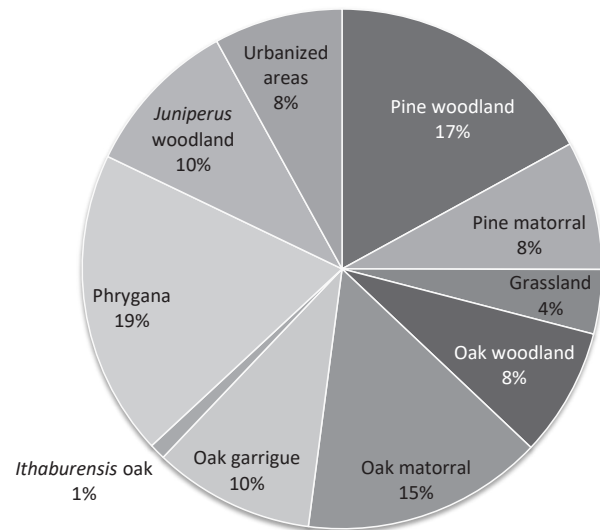


Figure A1. Habitats of Jabal Akroum. **A.** *Quercus coccifera* oak woodland. **B.** *Pinus brutia* pine woodland. **C.** Oak matorral. **D.** Pine matorral. **E.** *Juniperus excelsa* matorral. **F.** Oak garrigue. **G.** Grassland. **H.** *Sarcopoterium spinosum* phrygana.



*calliprinos*) oak arborescent matorral (F5.114) covered 15% of the area, oak garrigue (F6.21) covered 10%, and oak woodlands (G2.13) covered 8% and were spotted along the crest and on the eastern slopes of the mountain. In the oak woodland and oak arborescent matorral, the associated dominant tree species were *Pistacia palaestina* and *Phillyrea latifolia*, along with *Juniperus oxycedrus* shrubs. In oak garrigue habitat resulting from the degradation of evergreen forests, the same species are reduced to dwarf shrubs, not exceeding 1 m in height and with a low density. Phrygana of *Sarcopoterium spinosum* covered 19% of the area and exclusively thrived on the northern part of the mountain which has the lowest altitude, ranging between 300 to 850 m. *Juniperus excelsa* arborescent matorral (F5.1331) covered 10% of the area and was exclusively spotted on the southern part of the mountain, which has the highest altitude, ranging between 1100 and 1260 m. It is characterised by sparse trees of *Juniperus excelsa* in pure stands or associated with *Quercus coccifera*, which constitute a unique and rare association in Lebanon. This habitat is threatened as *J. excelsa* is a nationally endangered species due to illegal wood exploitation (Douaihy et al. 2016). Grasslands (E1.4) constituted spots scattered through the crest and eastern slopes and occupied a total of 4% of the area of the mountain. They were by far dominated by *Dactylis glomerata*, and secondarily by *Phleum montanum*. Remaining patches of woodland of *Quercus ithaburensis*



**Figure A2.** Relative areas occupied by each type of habitat on Jabal Akroum (Lebanon) in November 2019.

subsp. *ithaburensis* were spotted in the northern part of the mountain, covering less than 1%. This habitat is rare in Lebanon and occurs exclusively in this very northern area of Akkar, between Jabal Akroum and Nahr el-Kebir. Other patches were reported in the south of the country around Sarada (Mouterde 1966). More than 8% of the area of Jabal Akroum is urbanised (Fig. A2).