



A taxonomic snapshot of belowground organs in plants of Anatolian steppes

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Abstract The lack of information on plant traits limits our understanding of how plant species and communities will respond to ongoing global changes. The biodiversity-rich Anatolian steppes have remained unexplored in terms of belowground plant traits. We documented the distribution and representation of belowground organs (excluding roots that do not form a bud bank) in Anatolian steppe plants, categorizing them by taxonomic family and growth form. Comparisons and analyses were made using data from the published Flora of Türkiye. Our results show that one-fifth (736 taxa) of all Anatolian steppe plants and one-third (514 taxa) of polycarpic hemicryptophytes bear a belowground organ with clonality or perennation functions. The proportion of belowground organ types varied between growth forms, as polycarpic hemicryptophytes had mainly rhizomes or rootstocks whereas geophytes had bulbs. Some families, such as the Amaryllidaceae, Asparagaceae and Liliaceae, possessed a specific type of belowground

organ, while some others, including the Rosaceae, Caryophyllaceae and Asteraceae, had a higher diversity of belowground organ types. We conclude that the seasonal climate with cold winters and dry summers can be a driver of this belowground organ diversity in Anatolian steppes. The presence of bulbs, rhizomes and tubers appears to be phylogenetically clustered, with the representation of these organs differing between the monocot clade and the eudicot clade; indeed, bulbs and corms are, in this case, exclusive to monocot families. Further measurements of belowground plant traits in the field and laboratory are needed to fully understand the patterns and processes in Anatolian steppe ecosystems.

Keywords Anatolia · Belowground plant traits · Clonality · Perennation · Steppe vegetation · Temperate grassland biome

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Introduction

The functional trait approach is a widely used method in ecological research and provides a broad understanding of species interactions with each other and their environments (Garnier et al. 2016). In this context, studies involving belowground traits have also received increased attention in recent years. Consequently, our knowledge of belowground organs and traits has deepened for several ecosystems, including Mediterranean shrublands (Paula et al. 2016),

temperate region ecosystems (Klimešová et al. 2017) and savannas (Bombo et al. 2022), and even at the global level (Iversen et al. 2017; Pausas et al. 2018). Nevertheless, there are still many ecosystems that lack any information on belowground plant traits, as suggested by the lack of geographic representation in regional or global databases with information on belowground organs and traits (Tavşanoğlu and Pausas 2018; Kattge et al. 2020; Guerrero-Ramírez et al. 2021).

Unlike belowground plant traits, aboveground plant traits, such as the leaf, stem and seed traits, have been studied more frequently because they are easier to measure than belowground plant traits and because vegetation structure assessments rely on aboveground properties of plants (Moles et al. 2007; Díaz et al. 2016; Bruelheide et al. 2018). However, belowground traits can be equally or more important in comparison to aboveground traits, as they are determinants of the persistence of plants in many ecosystems and their role in ecosystem stability and function (Laliberté 2017). For example, many grassland species allocate a substantial amount of their biomass (i.e. carbon) to belowground organs with either short- or long-term persistence, enabling them to survive or tolerate disturbances or unfavorable seasonal conditions (Klimešová et al. 2018). Since belowground organs provide storage for carbohydrates or protection for buds, they also help to resprout after disturbances such as fire (Pausas et al. 2018). Some belowground organs, such as rhizomes, tubers and bulbs, are specialized structures that store energy and nutrients. Rhizomes, for instance, are horizontal underground stems that can produce new shoots and roots, allowing rapid vegetative propagation (Pausas et al. 2018). Tubers serve as energy reserves, packed with starches and other carbohydrates that allow regrowth after adverse events (Klimešová et al. 2019). Bulbs, another specialized storage organ found in many perennial plants, contain layers of nutrient-rich tissue that can support rapid regrowth once favorable conditions return (Klimešová et al. 2019; Wigley et al. 2020). Therefore, these belowground organs provide a survival advantage during periods of environmental stress, drought or herbivory and enable plant species to re-emerge post-disturbance, ensuring the continuity and resilience of the plant community. Therefore, neglecting belowground traits and organs in grassland ecosystems can result in underestimating their effect

on species interactions and ecosystem processes (Ottaviani et al. 2020).

Anatolian woodlands, shrublands and grasslands are among ecosystems that have never been studied in terms of belowground plant organs or traits. The Anatolian peninsula shows diverse climatic and topographic conditions and is an important biodiversity refugium and diversification centre for plant species (Şekercioğlu et al. 2011). Anatolia is also the meeting point of the Mediterranean, Caucasian and Irano-Anatolian biodiversity hotspots (Mittermeier et al. 2011). Consequently, the highly biodiverse Anatolia harbours more than 12,000 plant taxa with a high proportion of endemism (Şekercioğlu et al. 2011; Pils 2013). Among several key biodiversity areas defined in Anatolia, grasslands are the most extensive habitat type, covering 50% of the land area of these biodiversity-rich sites (Eken et al. 2016). Moreover, central Anatolian steppes have an endemism proportion of 30%, which includes several endemic genera (Kurt et al. 2006). Despite this extraordinary plant diversity, Anatolian steppes lack adequate conservation measures and are under threat of land-use changes and overgrazing (Şekercioğlu et al. 2011; Ambarlı et al. 2016). Besides habitat loss and fragmentation, climate change is predicted to pose an additional threat to biodiversity in Anatolian steppes in the near future (Ergüner et al. 2019).

Furthermore, although several taxonomic, systematic and ecological studies have been carried out in Anatolian steppes (e.g. Doğan and Akaydın 2005; Vural et al. 2006; Kenar et al. 2020; Özüdoğru et al. 2021), plant functional traits in this region have received little attention. To date, only a few studies have considered the functional traits of a few Anatolian steppe species (Yıldırım et al. 2012; Tavşanoğlu et al. 2015; Yeşilyurt et al. 2017), and plants of Anatolian steppes have not been studied in terms of belowground plant traits. Moreover, the lack of information regarding plant traits restricts our understanding of how plant species and communities of Anatolian steppes will respond to ongoing global changes. Therefore, in this study, as a first step to fill this gap, we aimed to document for Anatolian steppe plants, the taxonomic distribution and frequency of occurrence of belowground organs (roots that do not form a bud bank excluded) by compiling and analysing relevant data from the Flora of Turkey and the East Aegean Islands (hereafter referred to as the published

Flora of Türkiye – Davis 1965-1985 ; Davis et al. 1988). Because the vegetation of Anatolian steppes has long been subjected to various disturbance regimes, including herbivory and fire (Tavşanoğlu 2017), and as it experiences climates with strong temperature and precipitation seasonality (Peel et al. 2007), we expected to find great diversity of belowground organs in the plants of this region. Furthermore, we aimed to assess whether phylogenetic factors play a role in shaping the belowground organs of plants in Anatolian steppes.

Material and Methods

Study Area

Our study focuses on Anatolian steppes, which are part of the temperate grassland biome (Ambarlı et al. 2016). Our research encompassed four vegetation types in Anatolia, Türkiye: central Anatolian steppes, eastern Anatolian montane steppes, central and eastern Anatolian wooded steppes, and southeast Anatolian Mediterranean steppes. The study region aligns mainly with the Irano-Anatolian biodiversity hotspot and partly with the Mediterranean Basin hotspot (Mittermeier et al. 2011) and is part of the Irano-Turanian floristic region (Djamali et al. 2012). The Anatolian steppes exist under a variety of climate types. Specifically, central Anatolia is dominated by a cold semi-arid climate with cold winters and warm summers whereas eastern Anatolia experiences a humid continental climate with colder temperatures and comparatively warm summers. By contrast, southeastern Anatolia is characterized by a hot-summer Mediterranean climate (Peel et al. 2007). In the region, the precipitation regime varies considerably at the local scale due to the complex topography of the Anatolian peninsula. However, all areas within the Anatolian steppes and woody steppe regions experience precipitation seasonality, as distinct wet and dry periods can be recognized. The study area lacks a dominant soil type due to regional differences and substantial variability even at highly localized scales (Ambarlı et al. 2016). Spatial variability of climate and soil types created significant differences in vegetation types at the local scale (Kurt et al. 2006). Consequently, different steppe vegetation formations can coexist at the regional scale depending on local

microclimatic conditions and soil formations. The region was influenced by frequent wildfires after the end of the last glacial maximum and for most of the Holocene, the progressive shift from steppe vegetation to cropland coupled with an increase in domestic grazing have significantly limited natural fires in recent millennia (Tavşanoğlu 2017). At present, the region's disturbance regimes are predominantly influenced by human activities such as land conversion for crop production and domestic grazing.

Dataset

We compiled data on plant belowground organs in Anatolian steppes using species definitions in the published Flora of Türkiye (Davis 1965-1985; Davis et al. 1988). This Flora book series includes several plant traits of more than 3,500 plant taxa from Anatolian steppes, including whole-plant, regeneration, floral, and leaf traits (Ülgen and Tavşanoğlu, unpublished data). For this study, we used the growth form and belowground trait records in these books (Davis 1965-1985; Davis et al. 1988). In our study, we only included belowground organs except for roots without a bud bank. We followed the nomenclature of Davis (1965-1985) and Davis et al. (1988), incorporating taxonomic updates from the Taxonomic Name Resolution Service (Boyle et al. 2021) and the World Flora Online (WFO 2022).

Although the study area is dominated by steppe and woody steppe vegetation, different vegetation types can also be found in several locations in the study area, such as forests and wetlands. Therefore, instead of recording all species found within the study area, we carried out a filtering process according to the habitat of each species, with the aim of focusing solely on steppe and grassland plants. For this purpose, we took into consideration the habitat definitions in the published Flora of Türkiye (Davis 1965-1985; Davis et al. 1988). Accordingly, we did not include species only found in humid / wet meadows, wetlands, streams and lake shores, swamps, salt marshes, salty swamps, mixed deciduous forests, pine, cedar, spruce, and beech forests, maquis and garrigue areas in our dataset. Additionally, plant species known to be aquatic or semi-aquatic in character, non-native species that have been cultivated, hybrid species, and poorly understood or doubtful records were also excluded from our dataset.

Our dataset included the following growth forms: monocarpic hemicryptophyte, polycarpic hemicryptophyte, geophyte, subshrub (dwarf woody plant), and suffruticose (polycarpic perennial herb woody at the base; Table 1). The belowground organ types we included in our dataset were bulb, corm, rhizome, stolon, tuber, caudex and rootstock (Table 2). All of these organs bear buds and have a function in perennation, but only the first five allow plant individuals to reproduce clonally, and the latter two can only use these buds for resprouting (Pérez-Harguindeguy et al. 2013; Pausas et al. 2018; Klimešová et al. 2019). We assigned species with uncertain growth form descriptions (e.g. ‘perennial herb or subshrub’) into a ‘variable’ growth form category. Similarly, we also created a category named ‘uncategorized’ for taxa with belowground organs that lacked enough information about their origin (e.g. ‘root or rootstock’, ‘woody stock’) in the published Flora of Türkiye (Davis 1965-1985; Davis et al. 1988; Table 2). Since species descriptions provided detailed information about the belowground organs of plants in the published Flora of Türkiye, if a plant has any, we regarded each species without a description of any belowground organ as one without a belowground organ.

Data Assessment

To quantify the variability in belowground organ diversity among families, we calculated the Shannon diversity index for each family using the number of taxa nested in each belowground organ type (except ‘uncategorized’) in each family. For this analysis, we used the ‘diversity’ function in the ‘vegan’ R package (Oksanen et al. 2019). To compare Shannon values between clades, we performed Hutcheson’s t-test using the ‘ecolTest’ package (Salinas and Ramirez-Delgado 2021). We also performed a linear regression analysis to test whether there is an association between belowground organ diversity and the number of taxa with belowground organs for each family. To show the possible relationships between phylogenetic closeness and the presence of specific belowground organs, we constructed a phylogenetic tree of plant families, each with at least one taxon possessing a belowground organ. The phylogenetic tree was created using the ‘GBOTB.extended’ mega-tree implemented in the ‘V.PhyloMaker’ package (Jin and Qian 2019). In this tree, the phylogenetic relatedness was

Table 1 Definitions of growth forms used in this study. The definitions are based on Pérez-Harguindeguy et al. (2013) and Tavşanoğlu and Pausas (2018) Polycarpic perennial herbs are divided into two additional life form categories based on Raunkiaer’s life forms (Ellenberg and Mueller-Dombois 1967)

Growth form	Definition
Herbaceous	Monocarpic herbaceous plants
	Herbaceous plants growing vegetatively in the first or second growing season, then flowering and producing seeds in the last growing season before their death
	Polycarpic perennial
Woody	Polycarpic perennial
	Suffruticose
Variable	Subshrub
	Herbaceous or woody plants living for at least three growing seasons and reproducing more than once in their lifetime
	Herbaceous plants which can persist in unfavourable conditions with a bud-bearing stem base near the ground surface
	Geophyte
	Herbaceous plants which can persist in unfavourable conditions with buds located below ground
	Polycarpic perennial herbaceous plant woody at the base
	Polycarpic perennial dwarf woody plants less than 0.5 m
	Herbaceous or woody plants with a loose growth form definition in the published Flora of Türkiye (e.g. ‘biennial or perennial’, ‘annual, biennial or perennial’, ‘subshrub or suffruticose’, ‘subshrub or perennial herb’); this category includes only eight taxa.

Table 2 Belowground organ types occurring in Anatolian steppe plants. The definitions and functions are based on Pérez-Harguindeguy et al. (2013), Pausas et al. (2018), and Wigley et al. (2020)

Belowground organ type	Definition	Function
Bulb	Belowground stems with fleshy scale leaves	Carbohydrate storage; perennation; protecting axillary buds; multiplying (clonal)
Corm	Globose, thickened belowground stems	Carbohydrate storage; perennation; protecting axillary or terminal buds; multiplying (clonal)
Tuber	Thickened, mostly vertical belowground stems	Carbohydrate storage; perennation; axillary bud bearing, multiplying (clonal)
Rhizome	Perennial, horizontal belowground stems	Lateral spread; vegetative reproduction; ability to cope with shoot loss; perennation (clonal)
Stolon	Elongated horizontal aboveground stems	Producing independent plants via axillary bud growth and rooting; perennation (clonal)
Caudex	A stem structure that is surrounded by dead leaves or leaf bases and has one apical bud	Resprouting; perennation (non-clonal)
Rootstock	Swollen woody structures, including a high concentration of renewal buds (basal burl) or thickened root crown due to multiple resprouting events (root crown)	Bud bank; resprouting; perennation (non-clonal)
Uncategorized	Belowground organs with a loose definition in the published Flora of Türkiye (e.g. ‘rhizomes or roots’, ‘woody stock’)	

based on the APG4 classification of plants (Angiosperm Phylogeny Group 2016). We performed all analyses in the study in the R environment (R Core Team 2021).

Results

Of the 3,515 Anatolian steppe taxa recorded in our dataset based on the published Flora of Türkiye (Davis 1965-1985; Davis et al. 1988), 736 (20.9%) had belowground organs (the electronic supplementary material). Excluding annual herbs, the proportion of taxa with belowground organs rose to 26.4% among those with perennial life cycles only. Most plants in our dataset had belowground organs enabling clonality (i.e. belowground clonal organs), namely bulb, corm, rhizome, stolon and tuber. On the other hand, some species contained belowground organs that do not have the clonality function but support perennation and resprouting (i.e. non-clonal organs), such as caudex and rootstock. The majority of the belowground organs of Anatolian steppe plants were rhizome and rootstock (each accounted for 26.5%) and bulb (21.5%). Other belowground organs, such as tubers, caudices, stolons and corms, were less frequent in Anatolian

steppes, found in 6.9%, 5.3%, 2.9% and 2.7% of the plants with belowground organs, respectively (Table 3). Though, 7.7% of the total belowground organs of Anatolian steppe plants remain uncategorized according to our definition.

Nearly 60% of taxonomic families (44 out of 75) contained at least one species with a belowground organ (Table 3), with the highest number of such records found in the Asteraceae family (164), followed by the Amaryllidaceae (74) and then the Apiaceae (59 taxa). Some families were found to have a specific belowground organ type. For instance, all taxa in the Amaryllidaceae and Liliaceae and 95% in the Asparagaceae were bulbous whereas all taxa in the Araceae and Orchidaceae were tuberous, and 100% and 45.2% of taxa had a corm in the Colchicaceae and Iridaceae, respectively (Table 3). Similarly, when considering only taxa including a belowground organ, 100% of taxa in the Cyperaceae, 92% of the Campanulaceae, 83% of Poaceae and 35% of Asteraceae had a rhizome, and 52% of taxa in the Ranunculaceae were tuberous (Table 3). Moreover, 40.4% of Fabaceae and 29.2% of Caryophyllaceae taxa with belowground organs had a caudex. Likewise, 93.2% of Apiaceae, 61.6% of Asteraceae, and 44.7% of Fabaceae taxa with belowground organs had a rootstock. Of the taxa with a belowground organ in

Table 3 Distribution of taxa with different belowground organs across major clades and plant families in Anatolian steppes. The numbers presented are the numbers of taxa for each family per organ type. Only families with at least one taxon having a belowground organ were included. *N* is the total number of taxa in each family, *n* is the number of taxa with a belowground organ, and *H'* is the Shannon diversity index. 'Clon.' and 'Peren.' refer to clonality [%] and perennation [%], respectively, and represent the proportion of the number of taxa with belowground clonal organs and with belowground

perennating organs, respectively, to the total number of taxa in each family. Belowground organ abbreviations are defined as follows: 'b' – bulb, 'c' – corm, 'r' – rhizome, 's' – stolon, 't' – tuber, 'ca' – caudex, 'rs' – rootstock, and 'u' – uncategorized. Families that include both annual and perennial taxa are indicated with an asterisk (*); no asterisk means the corresponding family possesses only perennial taxa. The growth form data are based on Watson and Dallwitz (1991), Davis et al. (1965–1985), and World Flora Online (WFO 2022)

Clade / Family	Belowground organ									<i>n</i>	<i>N</i>	Clon. [%]	Peren. [%]	<i>H'</i>
	B	c	r	s	t	ca	rs	u						
Monocots	158	20	72	1	14	0	0	2	267	406	65.3	65.8	1.03	
Eudicots	0	0	123	20	37	39	194	54	467	3108	5.8	15.0	1.30	
Amaryllidaceae	74	0	0	0	0	0	0	0	74	74	100.0	100.0	0	
Apiaceae*	0	0	0	0	4	0	55	0	59	178	2.2	33.1	0.25	
Apocynaceae	0	0	0	0	0	0	1	0	1	5	0.0	20.0	0	
Araceae	0	0	0	0	7	0	0	0	7	7	100.0	100.0	0	
Aristolochiaceae	0	0	0	0	0	0	1	1	2	2	0.0	100.0	0	
Asparagaceae	40	0	0	0	0	0	0	0	40	42	95.2	95.2	0	
Asteraceae*	0	0	41	8	3	11	101	0	164	503	10.3	32.6	1.05	
Berberidaceae	0	0	0	0	1	0	0	0	1	2	50.0	50.0	0	
Boraginaceae*	0	0	4	0	0	0	0	5	9	157	2.5	5.7	0	
Brassicaceae*	0	0	4	1	0	0	0	4	9	247	2.0	3.6	0.50	
Campanulaceae*	0	0	12	1	0	0	0	0	13	59	22.0	22.0	0.27	
Caprifoliaceae	0	0	3	0	1	0	0	0	4	65	6.2	6.2	0.56	
Caryophyllaceae*	0	0	14	1	1	7	1	0	24	224	7.1	10.7	1.07	
Colchicaceae	0	6	0	0	0	0	0	0	6	6	100.0	100.0	0	
Convolvulaceae	0	0	0	0	0	0	0	4	4	32	0.0	12.5	0	
Crassulaceae*	0	0	0	2	1	0	3	0	6	27	11.1	22.2	1.01	
Cucurbitaceae*	0	0	0	0	3	0	0	0	3	3	100.0	100.0	0	
Cyperaceae*	0	0	11	0	0	0	0	0	11	14	78.6	78.6	0	
Euphorbiaceae*	0	0	0	0	1	0	0	2	3	38	2.6	7.9	0	
Fabaceae*	0	0	2	0	1	19	21	4	47	507	0.6	9.3	0.94	
Geraniaceae*	0	0	3	0	1	1	0	0	5	18	22.2	27.8	0.95	
Iridaceae	6	14	11	0	0	0	0	0	31	31	100.0	100.0	1.04	
Ixioliriaceae	1	0	0	0	0	0	0	0	1	1	100.0	100.0	0	
Juncaceae*	0	0	4	0	0	0	0	0	4	4	100.0	100.0	0	
Lamiaceae*	0	0	8	0	4	0	1	18	31	231	5.2	13.4	0.86	
Liliaceae	32	0	0	0	0	0	0	0	32	32	100.0	100.0	0	
Orchidaceae	0	0	0	0	7	0	0	0	7	7	100.0	100.0	0	
Orobanchaceae*	0	0	0	0	0	0	1	0	1	42	0.0	2.4	0	
Papaveraceae*	0	0	0	0	2	0	0	0	2	33	6.1	6.1	0	
Phrymaceae*	0	0	0	0	0	0	1	0	1	1	0.0	100.0	0	
Plantaginaceae*	0	0	1	3	0	0	0	0	4	55	7.3	7.3	0.56	
Poaceae*	5	0	38	1	0	0	0	2	46	179	24.6	25.7	0.46	
Polemoniaceae*	0	0	1	0	0	0	0	0	1	1	100.0	100.0	0	
Polygalaceae*	0	0	0	0	0	0	0	1	1	5	0.0	20.0	0	
Polygonaceae*	0	0	2	0	0	0	1	0	3	24	8.3	12.5	0.64	

Table 3 (continued)

Clade / Family	Belowground organ									<i>n</i>	<i>N</i>	Clon. [%]	Peren. [%]	<i>H'</i>
	B	c	r	s	t	ca	rs	u						
Primulaceae*	0	0	1	0	0	0	1	0	2	10	10.0	20.0	0.69	
Ranunculaceae*	0	0	8	0	13	0	0	3	24	80	26.3	30.0	0.66	
Rosaceae*	0	0	10	2	1	1	7	0	21	95	13.7	22.1	1.23	
Rubiaceae*	0	0	7	1	0	0	0	11	19	71	11.3	26.8	0.38	
Santalaceae*	0	0	0	0	0	0	0	1	1	12	0.0	8.3	0	
Saxifragaceae*	0	0	0	1	0	0	0	0	1	8	12.5	12.5	0	
Scrophulariaceae*	0	0	2	0	0	0	0	0	2	122	1.6	1.6	0	
Solanaceae*	0	0	0	0	0	0	0	1	1	8	0.0	12.5	0	
Xanthorrhoeaceae	0	0	8	0	0	0	0	0	8	9	88.9	88.9	0	

the Lamiaceae and Rubiaceae, most had uncategorized ones (58.1% and 57.9%, respectively).

Some families had a higher diversity of belowground organs, as indicated by analysis of Shannon's diversity, examples being the Rosaceae, Caryophyllaceae, Asteraceae, Iridaceae and Crassulaceae (all had $H' > 1.00$; Table 3). Among these families, Rosaceae had the highest belowground organ diversity ($H' = 1.23$), as all organs except bulbs and corms were observed in this family (Table 3). Although approximately 75% of belowground organs in the Fabaceae were rootstock or caudex, this family exhibited high diversity ($H' = 0.94$) with the presence of rhizomes and tubers, in addition to caudices and rootstocks (Table 3). Two major clades, both monocots and eudicots, showed a high level of diversity of belowground organs whereas the eudicot clade had significantly higher diversity than the monocot clade ($H' = 1.30$ and $H' = 1.03$, respectively, $t = -4.46$, $d.f. = 518.6$, $P < 0.0001$). Belowground organ diversity and the number of taxa with belowground organ within a family was slightly associated with each other, as linear regression analysis indicated a significant positive relationship ($R^2 = 0.25$, $P < 0.001$).

In some families, such as the Amaryllidaceae, Liliaceae and Orchidaceae, all taxa possessed at least one type of belowground clonal organ (Table 3). These families, along with many taxa in the Asparagaceae, had a geophyte growth form (the electronic supplementary material). However, some families, including many taxa with different growth forms, such as the Apiaceae and Asteraceae, also had a substantial representation of belowground organs with 33.1% and 32.6% of their taxa, respectively (Table 3). Moreover,

ca. 93% (55 of 59) and 97% (159 of 164) of taxa with a belowground organ in the Apiaceae and Asteraceae, respectively, were polycarpic hemicryptophytes (the electronic supplementary material). Indeed, among 1,795 polycarpic hemicryptophytes taxa among Anatolian steppe plants, 514 (28.6%) had a belowground organ. Apart from polycarpic hemicryptophytes (514) and geophytes (189 taxa), other growth forms had a lower frequency of belowground organs, including suffruticose plants (15 taxa), monocarpic hemicryptophytes (7 taxa), subshrubs (3 taxa) and plants categorized under 'variable' growth form (8 taxa; the electronic supplementary material). The proportion of belowground organ types differed among growth forms (Fig. 1). The most striking difference was between polycarpic hemicryptophytes and geophytes, where polycarpic hemicryptophytes mainly had taxa with rootstock or rhizomes, while geophytes most frequently had those with bulbs (Fig. 1).

Some belowground organs, such as tubers, rhizomes and stolons, were observed in several families across the phylogenetic tree of Anatolian steppe plants, but bulbs and corms were represented only by monocots (Fig. 2). Consequently, some phylogenetically closely related families exhibited similar belowground organ types, while others demonstrated divergent patterns (Fig. 2).

Discussion

Our study reveals that one-fifth of all plants and one-third of perennial herbaceous plants (i.e. monocarpic and polycarpic perennials, including

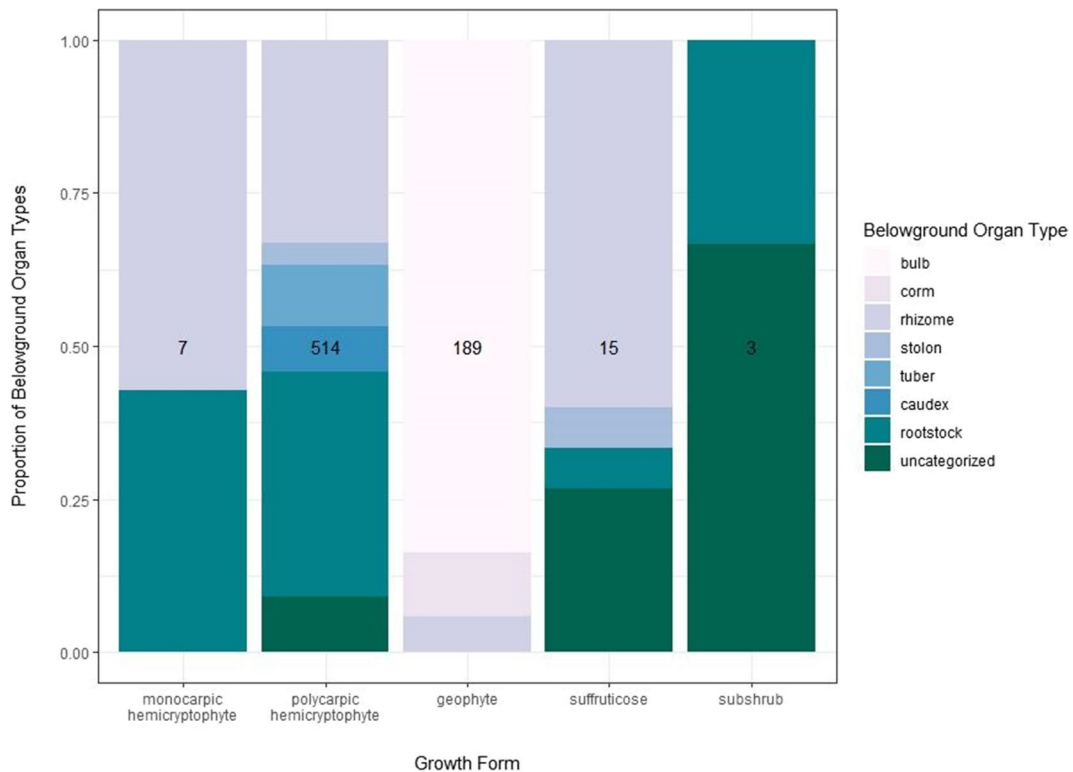


Fig. 1 Distribution of belowground organ types in taxa with different growth forms. The numbers on the bars refer to the number of taxa within each growth form. The ‘variable’ growth form category is not shown

geophytes) in the Anatolian steppes bear belowground clonal or perennating organs. The taxonomic distribution was broad, as 44 families contained at least one species with a belowground organ, but the frequency of occurrence of belowground organs varied among families. Our results on the frequency of belowground clonal organs in Anatolian steppe plants, especially in perennial herbs, suggest a high potential for the resilience of this vegetation after disturbance. In addition, the high prevalence of perennating organs among Anatolian steppe plants may reflect a selection or filtering process driven by harsh climatic conditions during winter (cold, snowy) and summer (hot or warm, dry) in central, eastern and southeastern Anatolia, where steppes are dominating. Indeed, many herbaceous plants have adapted to winter conditions by investing more carbohydrates into belowground perennating organs instead of aboveground biomass in regions with cold winters (Lubbe et al. 2021a). Aridity also shapes the belowground organ composition in

grassland plant communities, and dominant belowground organ types in a plant community can be selected through the aridity level of the ecosystem (Klimešová et al. 2023). Moreover, the overrepresentation of rhizomes and bulbs among Anatolian steppe plants with belowground organs may help the vegetative propagation of these plants after shoot loss under these unfavorable periods in Anatolian steppes. This result is in accordance with those observed in many other temperate grassland ecosystems, as rhizomes and bulbs are among the most frequently observed belowground organs in temperate grassland ecosystems globally (Pausas et al. 2018). However, our observation on the dominance of rhizomatous plants in Anatolian steppes partly contradicts the idea that increasing aridification would lead to the loss of rhizomatous plants from grassland communities (Klimešová et al. 2023). Still, given that vast expanses of the Anatolian steppes lie within arid or semi-arid zones, plant species within these ecosystems likely lean towards

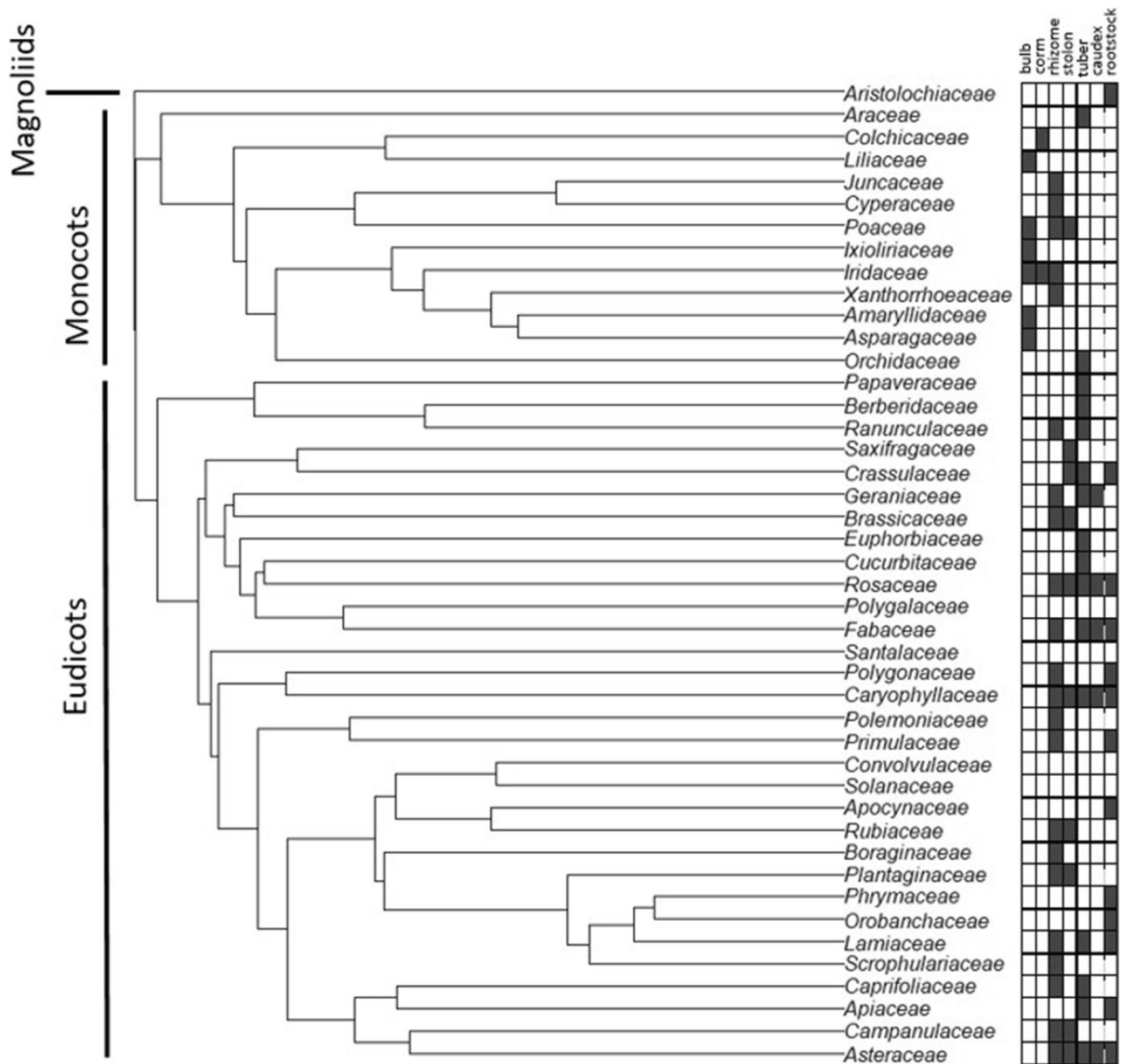


Fig. 2 Phylogenetic tree of plant families in the Anatolian steppes with the presence / absence of specific belowground organs. Only families with at least one taxon having a belowground organ were included. Black and white cells indicate the presence and absence of a specific belowground organ in the corresponding plant family, respectively. If a family's cells are

all empty, its belowground organ fall into the 'uncategorized' category. The tree was created using the V.PhyloMaker package (Jin and Qian 2019). The clades and phylogenetic relatedness are based on the APG4 classification of plants (Angiosperm Phylogeny Group 2016)

the resource-conserving end of the plant economic spectrum (De Micco and Aronne 2012). While clonal organs do not directly facilitate resource acquisition, they enhance plant persistence and support the storage of organic compounds (Pausas et al. 2018; Lubbe et al. 2021b); therefore, they can influence plant economics. Consequently, clonal organs

might give a distinct advantage to perennial plants contending with the challenging environmental conditions characteristic of Anatolian steppe habitats.

The frequency of occurrence of belowground organs varied among growth forms. Our documentation shows that geophytes and polycarpic hemicryptophytes are the growth forms in which belowground

organs are most frequently observed in the Anatolian steppes. This result is expected as polycarpic hemicryptophytes require belowground organs for perennation, contrasting with other growth forms where annual herbs can regenerate from seeds and many woody plants from aboveground parts. In our examination of growth forms, we observed that polycarpic hemicryptophytes predominantly form rootstocks and rhizomes as their primary belowground structures whereas geophytes frequently possess bulbs. This differentiation seems to be a byproduct of the phylogenetic organization of these growth forms. Notably, being a geophyte is prevalent among monocots whereas being a polycarpic hemicryptophyte is commonly associated with eudicots (Fig. 2).

In our study, we found that about 21% of all plants and about 29% of polycarpic hemicryptophytes plants in Anatolian steppes have a belowground organ. These values are lower than those reported for plants in Central Europe (53%, Klimešová et al. 2017) and China (40%, Ye et al. 2016) but higher than in Australia (9%, Zhang et al. 2018). However, this comparison should be approached with caution as our data is primarily based on species descriptions from the published Flora of Türkiye, potentially omitting information on some species. Our dataset might have also omitted root-sprouters that have the ability to sprout from adventitious buds on even the smallest root segments (Bartušková et al. 2017) because our main data source (Davis 1965-1985) does not include descriptions of this belowground organ type. However, in temperate regions, such plants constitute a part of regional floras (e.g. 10% in Czechia; Bartušková et al. 2017). Although we cannot specify the exact reasons for the discrepancies in percentages of plants with belowground organs across different regions, many drivers can be responsible for shaping belowground traits in plant species and communities worldwide. For example, phylogeny may have an effect on the trait structure of plant communities; indeed, the existence of belowground organs is phylogenetically conserved (Valverde-Barrantes et al. 2017).

Analysing the phylogenetic tree for Anatolian steppe plants, we also observed specific belowground organs clustered within certain taxonomic families. Notably, bulbs, rhizomes and tubers displayed signs of phylogenetic clustering, predominantly appearing within specific families. This clustering was most evident at the level of the two major angiosperm clades

in our dataset: monocots and eudicots, as, within the study area, bulbs and corms are exclusive to monocot families. This clustering also resulted in a higher Shannon diversity value in the eudicot clade than that of monocots in our study. This phylogenetic tree suggests that, for belowground organs of Anatolian steppe plants, a shared evolutionary history at the clade and the family level has played a more dominant role than adaptive convergence, and the corm and bulb organs have originated earlier in the evolution of angiosperms than other belowground organs. This observation is confirmed by the fact that families comprising solely perennial taxa often have a higher proportion of taxa with clonal or perennating belowground organs compared to most families with both annual and perennial species. Conversely, the observed high-level variation in belowground organs within the same family, such as in the Rosaceae and Asteraceae, may suggest that factors other than phylogeny may influence the structure of belowground organs in Anatolian steppe plants.

The lack of a strong relationship between belowground organ diversity and the number of taxa with a belowground organ within families also suggests that the diversity of belowground organs is driven by factors other than the number of species, possibly environmental ones. Indeed, sorting and filtering processes influenced by environmental factors are also important in shaping belowground trait patterns in plant communities. Climate may have a role in shaping clonal traits of plant species at larger (regional or biogeographic) scales (Chelli et al. 2019), and soil properties can also be related to the belowground traits representing fast and slow strategies through the resource conservation gradient (Lachaise et al. 2022). Moreover, the intensity and frequency of disturbances significantly influence the belowground trait structure in local plant communities (Benot et al. 2011; Takatsuki et al. 2018; Klimešová et al. 2021). Indeed, in many ecosystems of the world, fire and herbivory are major drivers of several plant traits, including belowground ones (Pausas et al. 2018; Takatsuki et al. 2018; Perkovich and Ward 2021). Such disturbances can be critical for the resilience and persistence of plant communities because they promote investment in belowground organs (Bombo et al. 2022).

At present, almost all uncultivated land in areas where steppe vegetation is present in Anatolia is under varying degrees of pressure from domestic grazing,

but these ecosystems were under natural grazing regimes by large herbivores before human civilization (Tavşanoğlu 2017). According to a study conducted in a steppe plant community in central Anatolia, this vegetation may be highly resilient to small-scale disturbances due to its significant proportion (35%) of resprouting perennial species (Özüdoğru et al. 2021). One of these well resprouting species, *Festuca valesiaca*, was found to decrease after long-term grazing in one Anatolian steppe rangeland (Fırıncıoğlu et al. 2009). This finding is unexpected as species capable of resprouting are often resilient to grazing in grassland habitats. However, abiotic conditions may alter the recovery potential of plant species (Linstädter and Baumann 2013); therefore, in drier environmental conditions, as in many parts of Anatolian steppes, the resilience of such species may be lower and disturbance-based mortality may increase. These contradictory observations suggest a need for further studies examining the disturbance response of species with or without belowground organs in Anatolian steppes. In addition to grazing, fire had also been a significant disturbance in Anatolian steppes, at least in the past. Although millennia of domestic grazing activity have removed fire from natural steppe areas on the Anatolian plateau (Tavşanoğlu 2017), the fiery past of this region during the early- and mid-Holocene periods (Turner et al. 2010) might have left a legacy that still influences the belowground trait structure of today's plant communities. Therefore, the presence of a belowground clonal organ might have been important for the long-term persistence of many perennial herbaceous species in the Anatolian steppes under past and present herbivore grazing and fire regimes.

Our study provides, for the first time, a summary of the diversity and distribution of belowground organs in plants of the Anatolian steppes. Our results reveal that a significant portion of Anatolian steppe plants have belowground organs with clonality or perennation functions. We conclude that the seasonal climate with cold winters and dry summers can be a driver of this belowground organ diversity and frequency in Anatolian steppes. On the other hand, our results also suggest the presence of a phylogenetic signal in belowground organs at higher taxonomic levels (i.e. clade and family). Because our dataset is based solely on the published Flora, we admit that there could be missing data on species with belowground organs. Another possible bias in our dataset may

arise from the fact that knowledge about some belowground organs (such as bulbs) is better compared to other types of organs. Nonetheless, our current dataset unveils the diversity of plant belowground organs in Anatolian steppes, marking a preliminary advancement in belowground trait research within the region. To better understand the belowground organ and trait diversity in Anatolian steppe communities, further studies need to be conducted in the field and laboratory, including the relationship between belowground traits and different environmental conditions such as climate, soil and grazing.

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Author Contributions C.Ü.: Investigation, Data Curation, Formal analysis, Writing – Original Draft, Writing.

Ç.T.: Conceptualization, Data Curation, Formal analysis, Writing – Original Draft, Writing, Supervision.

Data Availability The taxa with belowground organs in our study are listed in the supplementary file.

Declarations

Competing Interests The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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