

A first inventory of gypsum flora in the Palearctic and Australia

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Abstract. Gypseous substrates are well-recognised as supporting distinctive and unique flora assemblages, including numerous gypsum endemic (gypsophile) species. Along with these, others are also frequent although their presence is not restricted to gypsum; they show a clear preference for them (gypsocline). While this phenomenon (gypsophily) has been studied regionally, and various hypotheses put forward to explain it, there has been little global synthesis. We present a preliminary check-list on the gypsophile and gypsocline flora of the Palearctic and Australian areas as a part of a project to develop a global checklist of the World's gypsophytes, which can broaden our ecological and biogeographical understanding of these unique environments.

The database contains 935 taxa spanning 54 countries. The Irano-Turanian region –and to a lesser extent the Mediterranean region– emerged as the richest territories in terms of gypsophile species; this richness was much reduced in the Saharo-Arabian and, especially in the Eurosiberian regions.

The factors that can modulate the richness of gypsophytes in a region are discussed and have been distributed into four groups: a) geological and edaphic factors; b) factors linked to the insular nature of outcrops; c) climatic variables and their interaction with the soil; d) biogeographical factors. The importance of those factors linked to insularity and, especially, to water availability is emphasized. Because the soil structure of many gypsum outcrops reduces water ability to plants, such outcrops can be regarded as “dry-islands” surrounded by less xeric substrates. The fact that gypsophytes can be grouped within a few major flowering plant clades across continents, confirms their pre-adaptations to these harsh and unique environments. Our work provides a preliminary database for exploring ecological and biogeographic issues relating to gypsophily, and we hope it will stimulate global interest in these valuable ecosystems.

Keywords: edaphism; global check-list; gypsiculous; gypsophile; gypsophyte; gypsophily.

Un primer inventario de la flora gipsícola del Paleártico y de Australia

Resumen. Los sustratos yesíferos son sobradamente conocidos por presentar cortejos florísticos peculiares y exclusivos, lo que incluye a numerosos endemismos (especies gipsófilas). Junto a estas especies, aparecen otras también muy frecuentes cuya presencia no se restringe al yeso, pero hacia el que muestran una clara preferencia (gipsoclinas). Mientras que este fenómeno (gipsofilia) ha sido estudiado regionalmente, y se han sugerido varias hipótesis para explicarlo, apenas existen síntesis globales sobre el mismo. Aquí se ofrece un inventario preliminar de la flora gipsófila y gipsoclina de los territorios paleártico y australiano como parte de un proyecto que pretende desarrollar una checklist mundial, de manera que se contribuya a ampliar el conocimiento ecológico y biogeográfico de este ambiente único.

Este inventario incluye 935 taxa distribuidos por 54 países. La región irano-turaniana –y en menor medida la mediterránea– sobresale como el territorio más rico en especies gipsófilas; esta riqueza es mucho menor en el territorio saharo-arábigo y, especialmente, en la región eurosiberiana.

Se discuten los factores que modulan la riqueza en gipsófitos en las diferentes regiones distribuidos en cuatro categorías: a) factores geográficos; b) factores relacionados con la naturaleza insular de los afloramientos; c) variables climáticas y su interacción con el suelo; d) factores biogeográficos. Se resalta la importancia de los factores vinculados a la insularidad y, especialmente, la de aquellos que tienen que ver con la disponibilidad hídrica. Dado que las características de los suelos, reducen la disponibilidad hídrica, tales afloramientos deben considerarse como islas-xéricas rodeadas de sustratos menos xéricos. El hecho de que los gipsófitos enumerados aquí puedan agruparse en unos cuantos clados a lo largo de los diferentes continentes confirma su pre-adaptación a estos ambientes tan severos y únicos. Nuestro trabajo proporciona una base de

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datos preliminar para explorar cuestiones ecológicas y biogeográficas relacionadas con la gipsofilia, y esperamos que este recurso estimule el interés mundial por estos valiosos ecosistemas.

Palabras clave: edafismo; check-list global; gipsícola; gipsófilo; gipsófito; gipsofilia.

Introduction

Gypsum outcrops are widely distributed globally and strongly affect the flora that grows on them. In fact, many plant species only grow on this type of rock. This strong bond between soils originating from gypsum and the flora that grows on them is known as gypsophily (Parsons, 1976). Where the effect of the gypsum is pronounced, it represents a stressful edaphic environment, which restricts the number of plant species that can survive, and biological productivity may be severely limited (Mota & al., 2016; Pérez-García & al., 2017).

Another characteristic of these outcrops is their insular character. Thus, outcrops have been proposed to be ecological islands of specialized edaphic conditions, with a group of outcrops being an archipelago (Merlo & al., 1998; Pérez-García & al., 2003; Romão & Escudero, 2005; Mota & al., 2009, 2011; Martínez-Duro & al., 2010; Martínez-Hernández & al., 2013; Martínez-Nieto & al., 2013; Alexander & al., 2014; Moore & al., 2014; Escudero & al., 2015). The island biogeography of gypsum outcrops represents an emerging field of research (Mota, & al., 2013; Martínez-Hernández, 2013).

As a consequence of the two aforementioned characteristics (stressful environment and insular character), gypsum soils are often centres of plant endemism, a fact that has attracted the attention of many researchers who have tackled the subject of gypsophily from different angles. An essential question remains to reveal what factors determine the existence of gypsophile taxa. The answers supplied can be divided into two main groups: “chemical hypothesis”, emphasising the chemical and nutritional properties of the soil and “physical hypothesis” (Merlo & al., 1998). The latter is focused on physical factors such as the existence of a superficial crust from the recrystallization of gypsum, on which a briolichenic and algal cover grows, as well as the xeric water regime of the soils (Merlo & al., 1998; Moore & al., 2014; Escudero & al., 2015). However, these factors are not mutually exclusive, and it has been pointed out that each case will be the result of several factors acting simultaneously (Merlo & al., 1998; Moore & al., 2014; Escudero & al., 2015).

Another contested issue is how to best understand the gypsophile flora. For some researchers, it is composed of ‘specialists’ adapted to living competitively in that particular type of soil, and lacking competitive abilities outside them, that is, in more common and widely distributed substrates (Meyer, 1986). The opposite model is the ‘refugee’ one, in which gypsophytes are considered as stress-tolerant species, which lack special adaptations to gypsum soils but are able to

survive the harsh restrictions on them. These species have been displaced from other more common soils and are confined to the gypsum outcrops where less interspecific competition exists (Gankin & Major, 1964).

A new model has recently been proposed to address the issue: the narrow gypsophile/wide gypsophile model (Palacio & al., 2007; Escudero & al., 2015; Bolukbasi & al., 2016). According to this scheme, the most widely distributed gypsophytes would be specialists capable of accumulating Ca, S, N, Mg, P and Na, while the most stenochoric (narrow range) gypsophytes would be stress-tolerant species that find refuge from competition on gypsum soils.

Other authors have suggested that gypsophily is only a particular case of taxa adaptation to very xeric environments, where these characteristics are accentuated by edaphic nutritional imbalances. Certain plant lineages possess specific pre-adaptations that provide them with some advantages to survive in these environments (Merlo & al., 1998, 2011; Moore & al., 2014).

However, it is difficult to evaluate these models because gypsophily research has typically focused on just a few regions (Mota & al., 2016). The development of a global gypsophyte taxa database is a vital first step to test these models and theories. This research has that clear purpose and is related to the revisions carried out by Mota & al. (2016, 2017b) and Pérez-García & al. (2017).

The specific objectives of this research were: 1) to compile a floristic checklist of the gypsophytes from the Palaearctic and Australian territories, and of another one that also includes gypsocline taxa, since strict gypsophily is not always an easy character to establish (Mota & al., 2016); 2) to describe the richness patterns of the previously catalogued gypsophile flora and relate them to ecological and biogeographical factors; 3) to promote and extend such research to all territories with gypsophile flora in the world, and to stimulate the interest of botanists and ecologists worldwide.

Materials and methods

The study area of the present work was circumscribed to Australia, North and Central Eurasia and North Africa (see Figure 1 and Figure 2), as a first step towards a global inventory. From the biogeographic point of view, the Australian Kingdom, the African and Euro-Asian portion of the Holarctic Kingdom and the Asian portion of the Sudan-Zambesian Region are included (these biogeographic units and the following are based on Takhtajan [1986]). The result is 54 countries spanning 72,017,053 km².

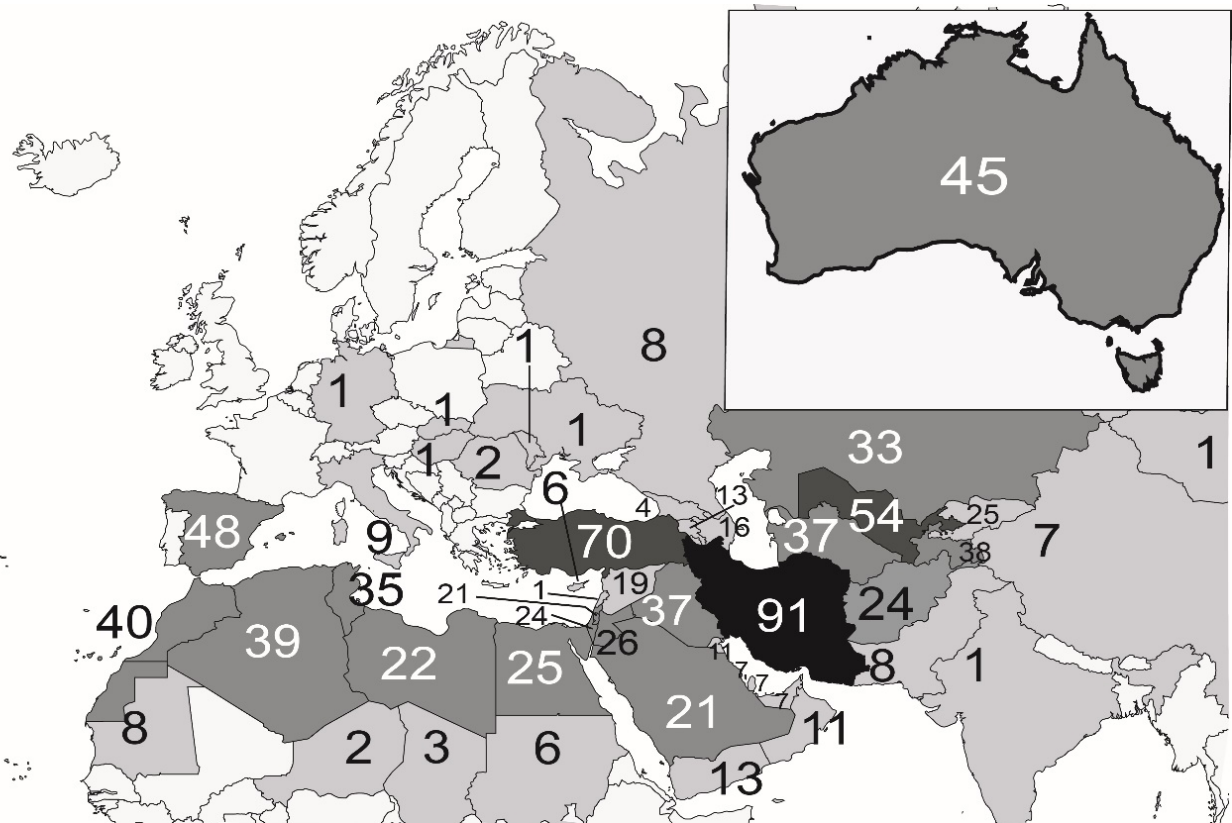


Figure 1. Number of gypsophytes in the countries of the study area. Color scale: black (> 74), dark grey (74-50), medium grey (49-20) and light grey (19-1).

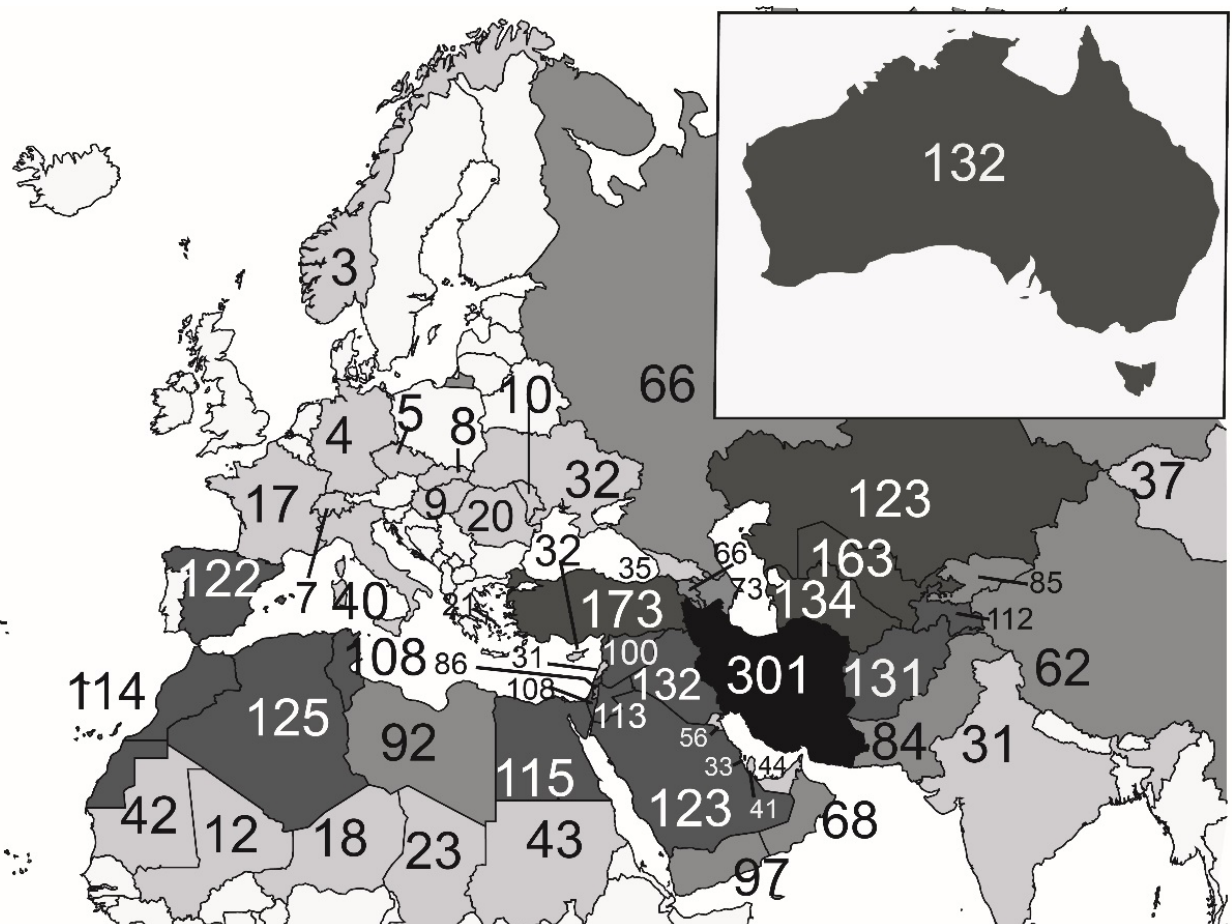


Figure 2. Number of gypsophytes and gypsoclines in the countries of the study area. Color scale: black (> 200), dark grey (199-100), medium grey (99-50) and light grey (49-1).

Compilation of the database of plants linked to gypsum substrates in the studied area involved a simple scheme of two categories, adapted from Mota & al. (2009, 2011). In the first category, according to their relationship with gypsum, are the “gypsophytes”: species that occur exclusively on, or with a clear preference for, gypsum, and which are very rarely found outside this substrate. They constitute the two maximum score levels of gypsophily according to the scale in Mota & al. (2009, 2011). On the other hand, the species that have been considered here as “gypsocline” taxa show a clear preference for gypsum, although they can also be found on other types of soils, which are also often nutritionally unbalanced for plants (e.g. marl, loess, chalk, etc.).

The inductive criterion indicated by Mota & al. (2011, 2016) was followed in order to compile the database; thus, after reviewing a large number of bibliographic sources (see Appendix I), those species indicated as such in floras and floristic catalogues were considered as gypsophile, as well as those considered as characteristic species of vegetal communities (syntaxa) developed on gypsum.

Appendix I lists all sources consulted from which the distribution of each taxon was established, complemented by the information collected on several websites: Global Biodiversity Information Facility, GBIF (<http://www.gbif.org/>), Euro+Med PlantBase (<http://www.emplantbase.org/>) and African Plants Database (<http://www.ville-ge.ch/musinfo/bd/cjb/africa/recherche.php>). At the specific and subspecific taxonomic levels nomenclature follow The Plant List (<http://www.theplantlist.org/>) and Euro+Med PlantBase (but with certain occasional exceptions). As

taxonomic scheme to assign genera to orders and families, the one proposed by the APG IV (2016) was followed. The family *Chenopodiaceae* is an exception because most chenopod specialists insist on keeping this separate from *Amaranthaceae* s.l. (Hernández-Ledesma & al. 2015).

According to the previously mentioned criteria, two floristic catalogues were compiled. The first one included gypsophytes, as defined above, whereas in the second, gypsocline species were added. The catalogues included both species and subspecies, but taxa of varietal rank and nothotaxa were excluded. The data were analysed using higher taxonomic ranks such as genera, families and orders. Two presence-absence matrices were obtained (one with gypsophytes and another with gypsophytes and gypsoclines); the analyses were carried out taking into account the information about the existing taxa in each country.

Figures 5, 6, 7 and 8 show the predominant bioclimate of each of the territories studied, since rainfall and temperature regimes have been identified as key aspects to understanding gypsophily (Mota & al., 2016). The data come from <http://www.globalbioclimatics.org/> (Worldwide Bioclimatic Classification System, 1996-2017, S. Rivas-Martínez & S. Rivas-Sáenz, Phytosociological Research Center, Spain. <http://www.globalbioclimatics.org>).

It should be noted that the results obtained here are preliminary and as the database is updated with new bibliographic sources and the knowledge of regional experts, they may experience some variations. These could become important when the study area is expanded to new and wider territories.

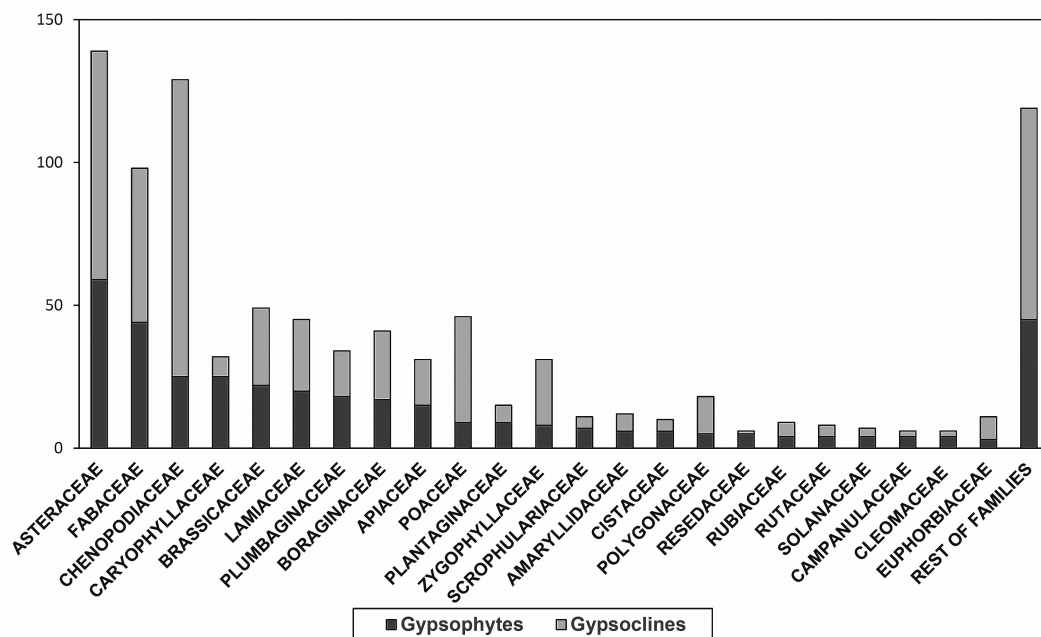


Figure 3. Distribution of taxa by families.

Results

In the study area, the gypsophytes catalogue contains 378 gypsophile taxa, at specific or subspecific level, belonging to

172 genera and 52 families. The gypsophytes+gypsoclines catalogue is composed of 935 species or subspecies, belonging to 349 genera and 70 families. Appendix II shows the two matrices for the 54 countries used for the analyses.

Appendix III and Figure 3 show the distribution of taxa by families in both catalogues. In the case of the gypsophytes list, the most represented family is *Asteraceae* (with 59 taxa), followed by *Fabaceae* (44) and *Caryophyllaceae* (25). In the gypsophytes+gypsoclinal catalogue, *Asteraceae* is the most speciose (139) followed by *Chenopodiaceae* (129 taxa) and *Fabaceae* (98). There is some overlap between the two lists in the ranking of the families with the greatest number of species (Appendix III). In both cases, the six largest families filled more than half of the species.

It is noteworthy that the inclusion of halo-gypsophyte taxa increases representation of *Chenopodiaceae*. There are eleven families represented in the gypsophytes list with a single species, and 18 when referring to the gypsophytes+gypsoclinal inventory. There is a clear dominance of just a few orders: *Caryophyllales* (80 taxa), *Asterales* (66), *Fabales* (45), *Lamiales* (39) and *Brassicales* (31) that filled more than two thirds represented roughly 75 % of all taxa. The prevalence of these orders is also observed in the gypsophytes+gypsoclinal catalogue.

The most widely represented genus in the gypsophytes inventory is *Astragalus* (with 25 taxa), followed by *Gypsophila* (19) and *Limonium* (14) (see Appendix IV). In the gypsophytes+gypsoclinal listing there is also a majority of species belonging to these genera, but changing the order: *Astragalus* (with 60 taxa), *Limonium* (23) and *Gypsophila* (21) genus. But

inclusion of halo-gypsophyte taxa increases the presence of the *Salsola* genus and its segregates (see Akhani & al., 2007, 2017) that together added up to 28 taxa. There are 97 genera with only one taxa represented on the gypsophyte list. A total of 197 genera can be found in the gypsophytes+gypsoclinal catalogue. Major differences between the lists resulted from the 177 genera present in gypsophytes+gypsoclinal catalogue but lacking in the gypsophytes one.

The distribution of the gypsophytes is gathered in Appendix V, and it is showed graphically in Figure 1 and Figure 4. The country with the highest number of gypsophytes is Iran (with 91 taxa), followed by Turkey (70), Uzbekistan (54), Spain (48) and Australia (45). If the gypsophytes+gypsoclinal inventory is considered (Figure 2 and Figure 4), the highest value corresponds to Iran with 301 taxa, followed by Turkey (173), Uzbekistan (163), Turkmenistan (134) and Australia (132). In both lists the five richest countries encompass more than two-thirds of the taxa, i.e. there is a strong spatial aggregation around some regions which are particularly rich in this type of taxa. On the other hand, countries from the north of Eurasia are poor in gypsoclinal and practically without gypsophytes. Those Saharian countries with lands neighbouring the Mediterranean Sea have a moderate number of gypsophytes, while the non-coastal countries of the Mediterranean are really poor in gypsophytes

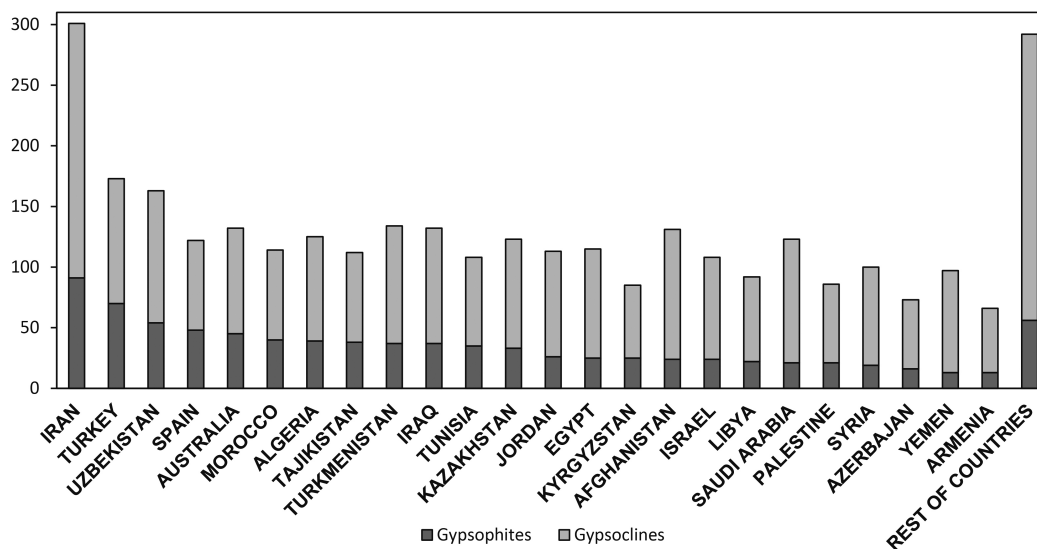


Figure 4. Distribution of taxa by countries.

Discussion

The gypsicolous flora of the studied area shows a clear taxonomic aggregation pattern: the majority of the gypsophytes and gypsoclinal are located within a few major flowering plant clades: *Asterales*, *Fabales*, *Caryophyllales* and *Brassicales*. That pattern seems clearly related to the gypsophily phenomenon, since it is more pronounced if

only gypsophytes are considered, rather than gypsoclinal. In the *Asterales* case, this can be explained by alluding to the extraordinary diversification of this order which has allowed it to thrive in almost all types of habitats.

For other orders, it seems that certain traits that aid survival in gypsum were inherited from ancestors who did not live in gypsum and for which these traits conferred evolutionary advantages over

other environmental stressors (pre-adaptations). Such explanations of certain species' success in the gypsum outcrops have been proposed since the times of Duvigneaud & Denaeyer-De Smet (1966). In the *Caryophyllales* order, some of them have druses (calcium oxalate crystals, e.g. *Gypsophila struthium*) in different tissues, a trait that could be selected evolutionarily due to their role in the defense against herbivores (Molano-Flores & al., 2001); in the case of plants on gypsum soils this would allow them to accumulate excess of calcium, which is called the accumulating strategy (Merlo & al., 2011; Moore & al., 2014). Other genera in this order, such as *Limonium* and *Frankenia*, follow a different strategy: extrusion, through which they expel the excesses of certain nutrients. It is evident that this trait is an inheritance of halophile lineages, which now allows some species to thrive on gypsum (Merlo & al., 2011; Moore & al., 2014). In the *Fabales* case, some of them can develop a great capacity for Ca and S accumulation (Moore & al., 2014). Symbiosis with *Rhizobium* is an adaptive advantage within this clade to thrive in N poor soils (Werner & al., 2015), such as those of gypsum (Rincón & al., 2008; Oyonarte & al., 2008; Boiscou & al., 2013). As regards *Brassicales*, some of the lineages possess a third strategy: the preadaptation of being rich in secondary metabolites which contain significant amounts of sulfur (Moore & al., 2014) and a great ability to obtain soil N (Mota & al., 2017a). Finally, a fourth strategy can be cited: avoidance. Avoiders are able to finely control ionic import and therefore, are able to survive on very poor and oligotrophic soils (Moore & al., 2014); the relatively large amount in gypsophytes of some lineages of *Cistaceae*, such as the *Helianthemum* genus, could represent this strategy.

Although gypsum outcrops are abundant and widely distributed throughout the planet, many of them do not support specialized gypsophile flora. To explore this further we now examine what factors may underpin gypsophyte richness of a country or region.

Geological and edaphic factors

A lot has been discussed about the required gypsum quantity in soil in order for gypsophilous plants to be present or in order for them to dominate vegetation coverage (see Mota & al. [2016] for details). During the compilation of this inventory, we rarely found data that relate the flora or vegetation to the gypsum content of the soil (cf. Mota & al., 2016). Furthermore, the existence of bi-edaphic plants shared between gypsum and other substrates such as dolomite, loess, chalk, salt, etc. (e.g. Mota & al., 1993, 2008, 2017b) is quite common. In this regard, the relation between gypsum and sodium chloride deserves a special mention: both minerals are often

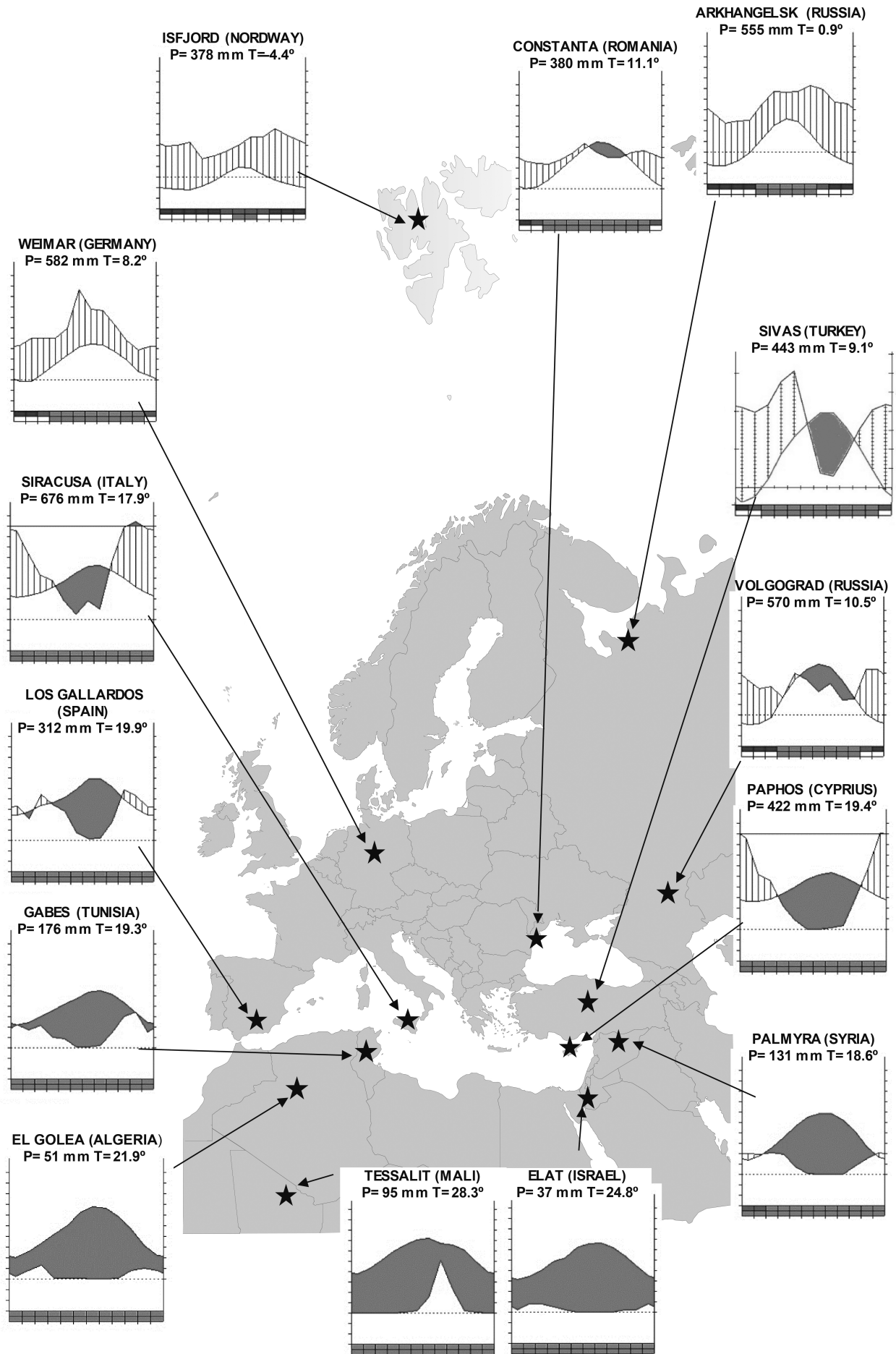
present together in the same soil (e.g. Esteve & Varo, 1975; Escudero & al., 2000; Waisel, 1972). Different terms related to this mixture have been used: "halophytic gypsophiles" (Parsons, 1976), "gypso-halophytic species" (Denaeyer-De Smet, 1970) or "halothiophores" (Duvigneaud & Denaeyer-De Smet, 1968). This can represent a major problem when establishing a list of true gypsophytes. In fact, while the proportion of gypsophytes versus gypsophytes + gypsoclines is 18.9% for the *Chenopodiaceae*, it rises almost 80% for the *Caryophyllaceae* and almost reaches 70% in the case of the *Plantaginaceae*. These differences are probably due to the high number of halo-gypsophytes, in the halophyte-rich family *Chenopodiaceae*, especially the *Salsola* genus and its segregates (Akhani & al. 2007, 2017).

It could be said that the presence of sodium chloride masks the effect of gypsum and could establish an asymmetric relation. Genuinely halophyte plants can develop in environments where there is a mix of salt and gypsum, and even penetrate gypsiferous outcrops. On the contrary, the opposite phenomenon is less common. To explore this contrasting behaviour by analysing our lists, especially the gypsocline species list, would be of great interest.

Insular character of gypsum outcrops

The fact that gypsum outcrops can be considered "habitat-islands" implies that species-area relations characteristic of insular environments could be documented (Martínez-Hernández, 2013; Mota & al., 2013, 2017b). Therefore, larger outcrops should possess more gypsophytes and more species in general. In the case of gypsum outcrops from the Iberian southeast, Martínez-Hernández (2013) demonstrated these relations (with some nuances), although it is early to generalize. The relationship between the number of gypsophytes of the different territories or countries and the area of the gypsum outcrops present can help to better understand this type of ecological relationship. However, the paucity of data on gypsum extent, have dissuaded us from carrying out a first attempt.

The insular nature of the gypsum outcrops has many parallels with other islands-within-the-mainland, as is the case of the "islands of height" that are the mountains. For the case of isolated mountains surrounded by radically different lowland environments, the concept of "sky-island" (Heald, 1967; Riemann & Ezcurra, 2007) was proposed. Since gypsum areas are clearly distinguishable from neighbouring substrates, among other things due to the harsh water stress that the plants growing there undergo compared to the surrounding ones, and drawing a parallelism with the sky-islands, gypsum outcrops could be considered as dry-islands.



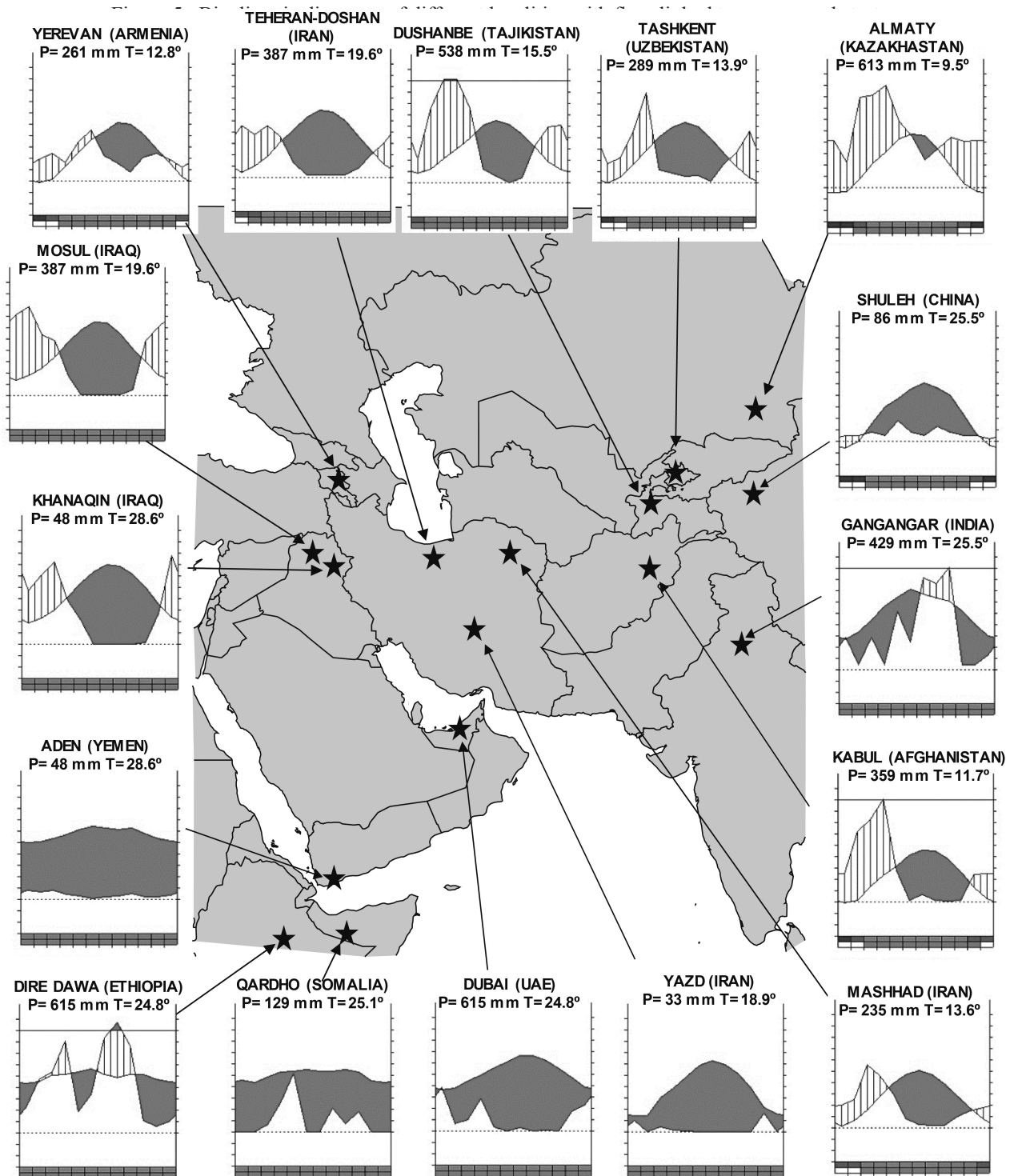


Figure 6. Bioclimatic diagrams of different localities with flora linked to gypsum substrates, from the Middle East, Central Asia and the Horn (Retrieved from <http://globalbioclimatics.org>).

Climate-soil interactions

From our analysis, it does not seem probable that temperature could be the main condition for the establishment of a gypsophilous flora, as there are gypsophytes in hot deserts and cold steppes; neither the degree of continentality, as there are rich gypsophilous floras in coastal shores and in the center of Eurasia; nor does altitudinal range seem to be a major determinant. Although there is a certain preference in gypsophilous flora for lowlands—maybe because erosive processes that wash gypsum increase with altitude (Cucchi

& al., 1998)—, there are gypsophytes in high lands of the Central Asian Mountains (Komarov, 1934-1964). But if temperature is not an important factor, water availability can be. There are many evidences to suggest that the factor with higher influence could be linked to drought (cf. Merlo & al., 2011; Linares & al., 2015). This could be reinforced by other physical factors in addition to mineral unbalance and the poverty of this type of soil. If one examines the bioclimatic diagrams of Figures 5-8, it is quite evident that the gypsophytes are concentrated in territories subject to a period of marked drought, almost always coinciding

with very dry summers. Nevertheless, gypsophile flora also exists in more northern latitudes, although it is much more sporadic and restricted to special topographic sites. These territories could be important refuges for flora of a more xerophilous nature that can find accommodation in open and partially depopulated zones like dry rupicolous environments (Mota, 2007). These environments are major locations for some taxa in very humid areas such as the jungles of Oaxaca (Zamudio & Studnicka, 2000). As stated by Pérez-García & al. (2017), gypsum outcrops act as a refuges for these xero-thermophilic taxa absent (or almost) from the surrounding non-gypsiculous areas with a scattered and sparse vegetation cover (Mota & al., 2007). The detection of flora linked to gypsum barrens amidst more humid and northern territories than those usually known is a key contribution of this research.

Another fact to consider related to the unusual geological outcrops is the existence of bi-edaphic taxa. Gypsum shares many floristic elements with dolomite, loess, chalk, marls, etc (Mota & al., 2017b). Such would be the cases of *Jurinea pinnata* (Pers.) DC. on dolomite and gypsum (Salmerón-Sánchez & al., 2014), *Pteranthus dichotomus* Forssk. on marl and gypsum (Mota & al., 2004; Boukhris & Lossaint, 1975), *Lamyropappus schakaptaricus* (B. Fedtsch.) Knorr. & Tamamsch on chalk and gypsum (Komarov, 1934-1964), *Astragalus namanganicus* Popov on loess and gypsum (Komarov, 1934-1964) or *Astragalus assadii* Maassoumi & Podlech on serpentines and gypsum (Podlech, 1988). From all of the above-mentioned, it follows again that gypsum is an extremely edaphoxeric environment, which subjects plants to an extraordinary water stress in which few species can thrive. These evidences point again to the hydric imbalance as a limiting factor (Merlo & al., 2011).

Biogeographical and palaeobotanical factors

Some biogeographic patterns can be inferred from among the distributions and abundances in the examined gypsophytes. Firstly, the northern gypsum outcrops of Eurasia, with some exceptions, lack of gypsophytes. This poverty is in line with the scarcity of endemism and stenochoric flora in such latitudes, as a consequence of the Rapoport rule (Rapoport, 1982) according to which the geographic extension of the species increases with the latitude. This is the reason why there are fewer stenochorous taxa and endemics in circumpolar areas. Due to the glaciations, another detail to consider is that the outcrops of these areas have been free of the ice cap only for a few thousand years. The current climate does not help the appearance of gypsophytes in these regions, although the presence of them has been described (e.g. *Gypsophila uralensis* Less. *subsp. pinegensis* (Perf.) R. Kam.) as have a forests associated with the gypsum outcrops of these territories (Tuyukina, 2009).

Further south, the temperate deserts and steppes of the Irano-Turanian region are the richest gypsophytes and gypsoclines zone in the study area (Figures 1 and 2). The cause of this extraordinary richness is likely

to be found in the fact that the deserts of Central Asia are among the oldest on earth (Caves & al., 2016). These deserts have maintained conditions of water restriction for 23 million years which, added to those imposed by the substrate, have given rise to a rich gypsophilous flora. The Mediterranean region, without reaching the richness of the Central Asian and Iranian Plateau outcrops, also shows a flora with a high number of gypsophytes. Like the Irano-Turanian region, the Mediterranean has been moderately affected by the glaciations and both constitute the northern portion of the Tethyan subkingdom.

Even further south, in the Sahara and Arabian deserts, a curious phenomenon is observed: the number of gypsophytes decreases. Something similar is observed in Australia since most gypsophile taxa are located in the southwest (South West Australian Region), not in the Outback deserts (Ereman Region). This pattern conforms to overall species richness, with the South West Australian Region well-documented as a global hotspot of narrow-range endemism and species richness (Hopper & Gioa, 2004). This could be contradictory, although aridity causes gypsophily, extreme aridity does not. In addition, the more arid a climatic regime is, the more blurred seems to be the differentiation between gypsophytes and halophytes. It should be noted that in extremely arid climates plants can adopt physiological strategies that allow them to survive in both salt and gypsum environments. The extruder strategy (Merlo & al., 2011; Moore & al., 2014) could be one of them. In relation to the above, there may also be other alternative explanations such as a lesser extent of gypsum outcrops or soils, a hypothesis that does not seem to be true, at least for the Sahara (Le Houréau, 1995).

Another possible explanation is related to desert endemism. According to this idea, the great monotony and scarce heterogeneity (at least when compared to the Mediterranean climate regions) of the deserts favours the existence of widely distributed taxa while local endemics are scarce, except in a few mountainous localities (cf. Ozenda, 2004) or other specialized habitats (e.g. desert springs; Fensham & al. 2011). This idea is supported by the fact that the gypsophile component of the Saharo-Arabian flora, which fulfills this pattern, is composed of widely distributed plants. This model is adapted to several species whose distribution ranges almost from the Atlantic to the Middle East (*Erodium glaucophyllum* (L.) L'Hér., *Herniaria hemistemon* J. Gay, etc.).

Another explanation, compatible with the two previous ones, resides in the effects of the insular character of the gypsum outcrops. It is likely that the majority of the gypsum of this type of biome comes from Holocene sabkha, and therefore the areas are small and adjacent to large deposits of other salts including NaCl (Aref & al., 1997; Benison & Goldstein, 2001). As already evidenced in the southeast of Spain (Martínez-Hernández, 2013), small gypsum outcrops close to saline materials could be impoverished in genuine gypsophytes and gypsotolerant halophiles could invade them. If we look at the data provided here, it seems evident that the number of gypsophiles declines in areas with extremely

arid climates although the available information is still very preliminary. This is a pattern that should be more carefully examined in the future, but preliminary analysis points toward the degree of isolation, the surface of the outcrops and their edaphic nature, especially the presence of salts other than CaSO_4 , as key factors.

Close to the equator, it is possible to find that in the deserts lower latitudes there are gypsum outcrops, but very few references to gypsophytes. Probably, the greater rainfall in the subtropical and equatorial zone diminishes the stressful effect of gypsum. However, there is another aspect whose effects would have to be separated from the latitudinal gradient *per*

se, and has to do with the rainfall regime and the different climates prevailing in these large regions. As already mentioned, there are gypsum outcrops in Mediterranean climates and others under tropical climates. If water stress is one of the key factors to unravel a phenomenon as complex as gypsophily, the seasonal regime of precipitation is probably the key. It is interesting to note the minimal role played by the seasonal precipitation regime in the investigation of the gypsophilous flora (Mota & *al.*, 2016), when outcrops with gypsophytes are present under a multitude of climatic conditions, as can be seen in the bioclimatic diagrams shown in Figures 5, 6 and 7.

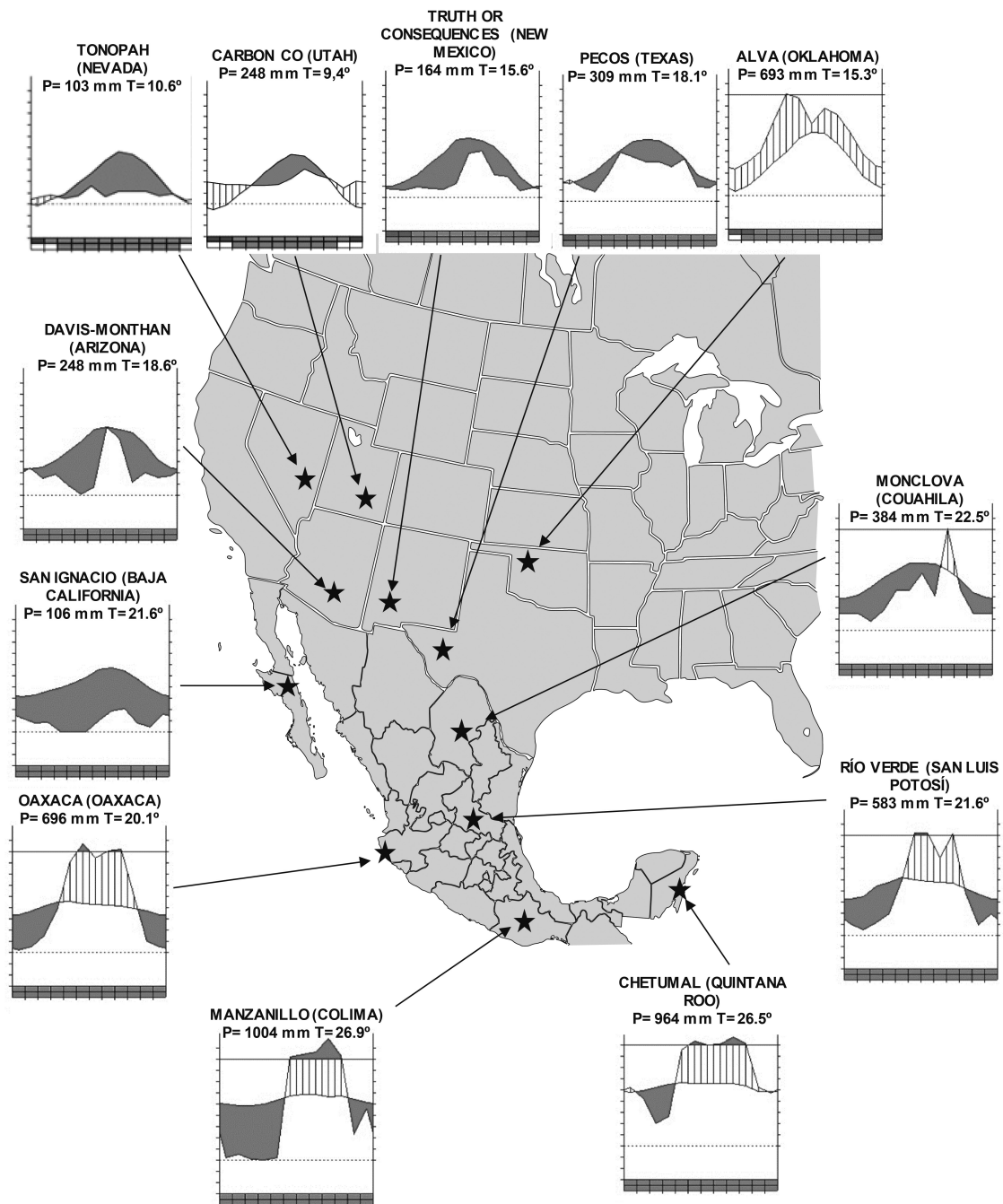


Figure 7. Bioclimatic diagrams of different localities with flora linked to gypsum substrates, from North America (Retrieved from <http://globalbioclimatics.org>).

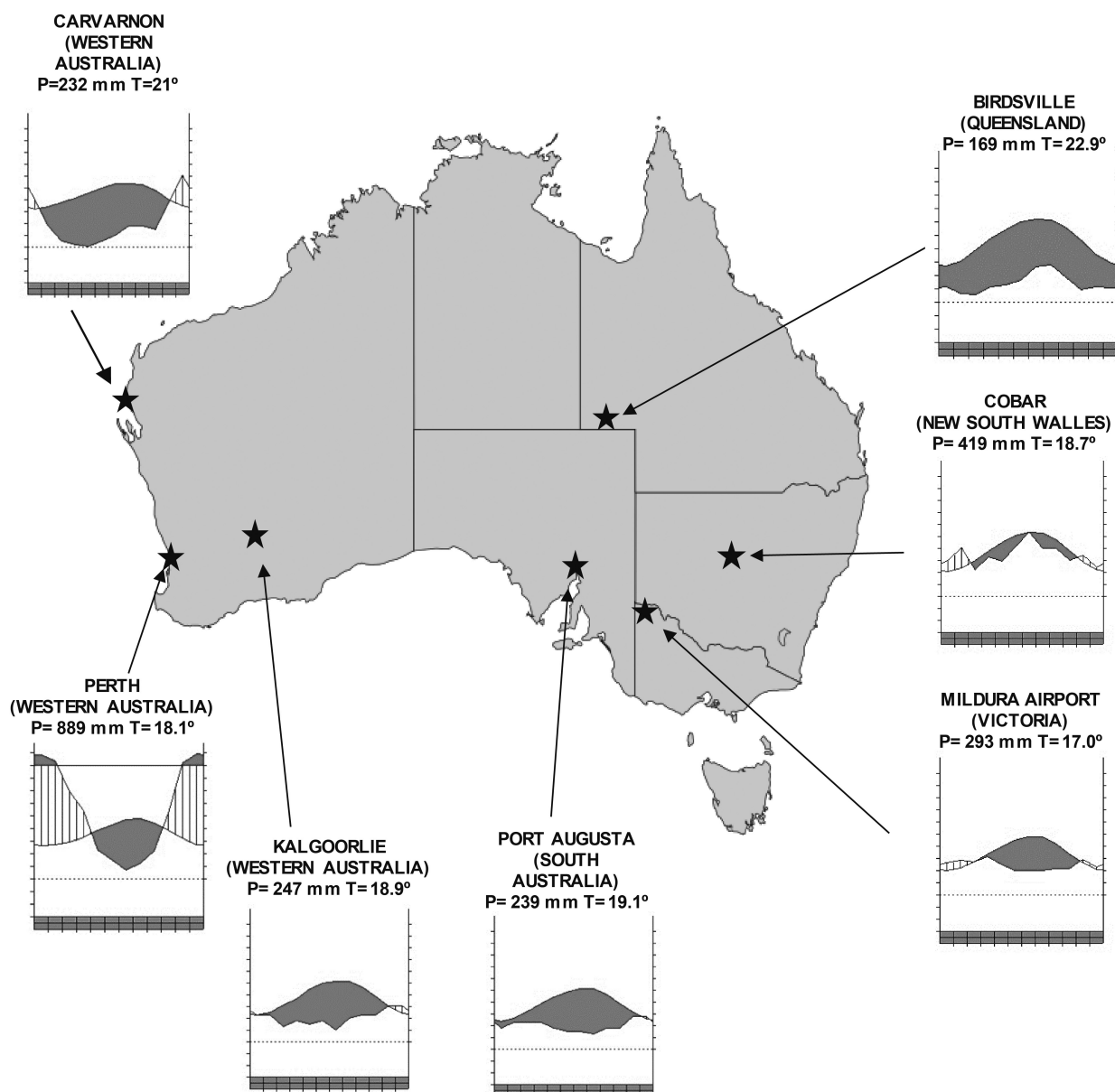


Figure 8. Bioclimatic diagrams of different localities with flora linked to gypsum substrates, from Australia (Retrieved from <http://globalbioclimatics.org>).

Implications for Conservation Biogeography

Not only are gypsophytes present under a wide variety of climatic conditions, but they also show a wide variety of chorological typologies as eurichoric or stenochoric. The latter ones are concentrated in some areas, true gypsophile hot spots, such as Sorbas Basin (Spain), Kepen area (Turkey), some Iranian areas (Western Semnan province, the zone between Zanjan and East Azarbaijan provinces and areas in Ilam and Khuzestan provinces), Guissar Range (Uzbekistan and Tajikistan), Köýtendag Range (Turkmenistan and Uzbekistan), Nugal Valley (Somalia) (Mota & *al.*, 2011; Yildirimli, 2012; Akhani, 2004; Eftekhari & Assadi, 2011; Komarov, 1934-1964; Thulin 1993-2006). Future studies of such localities and their gypsophytes can shed much light on the gypsophily phenomenon.

However, to the extent that advances are made in the knowledge of the gypsophile flora of the different territories and accurate information is available on the outcrops, this field of research should be explored given that it will be fundamental for the conservation of the endemic gypsum flora, which can be seriously affected by mining and, therefore, by the decrease in the extent of the outcrops (Mota & *al.*, 2011; Martínez-Hernández & *al.*, 2015).

Conclusions

Gypsum outcrops in the studied area show a greater richness in the northern part of the Tethyan subkingdom (the Mediterranean region and, especially, the Irano-Turanian region), while they are scarce in the Saharo-

Arabian region and almost non-existent in the Eurosiberian one. The extraordinary richness of the Irano-Turanian outcrops might result from the large expansion of gypsum formations associated with great antiquity of the regime of aridity prevailing in such territories. The poverty of Eurosiberian outcrops runs in parallel with that of the whole flora of the region. The small number of Saharo-Arabian gypsophytes might be explained in ecophysiological terms, or due to the low environmental heterogeneity or by the nature of many of their outcrops (Holocene sabkha).

The gypsum flora of the studied area shows a pattern of taxonomic aggregation: the majority of the gypsophytes and gypsoclines are located within a few major flowering plant clades, which coincides with previous studies and can be interpreted, in most cases, as the result of formerly related preadaptations.

Gypsum outcrops are widely distributed globally, but the existence of gypsophile taxa is much more restricted. Factors that modulate the richness of gypsophytes in a given region could be grouped into the following four groups: a) geological and edaphic factors, *i.e.* “quantity and quality” of gypsiculous materials; b) those linked to the surface area and insular character of the outcrops (“edaphic islands” size, etc.); c) climatic and the interaction of these with the soil (especially water availability); d) palaeobotanical and biogeographic. Among all of them, water availability seems to have the greatest influence.

Several issues remain open. The first one is related to the number of existing gypsophytes; according to

this study’s data, 378 species, belonging to 172 genera and 52 families, are serious candidates to appear in the checklist of the study area. The numbers will increase when the global checklist is developed, incorporating other territories such as the Americas and tropical Africa.

On the other hand, the interaction between climatic regime and gypsophily is far from being understood. It is clear that gypsophytes occur under different climatic regimes (temperate, Mediterranean, tropical and desertic –warm and cold–). However, the development of a global checklist will be critical to elucidate the mechanisms underlying gypsophily.

Only the involvement of a greater number of local and regional experts may make it possible to have a comprehensive gypsophile species checklist. And only from this final checklist will biogeographic and macroecological studies occur which provide a greater understanding of this global geobotanical phenomenon.

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Supplementary material

Supplement 1. Bibliographical sources.

Supplement 2. Check-list of flora. Main data matrix.

Supplement 3. Number of taxa by Families and orders.

Supplement 4. Number of taxa by Genera.

Supplement 5. Number of taxa by countries.