

*Chapter*

## THE ECOLOGY, ASSEMBLY AND EVOLUTION OF GYPSOPHILE FLORAS

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### ABSTRACT

Gypsum ( $\text{CaSO}_4 \cdot 2\text{H}_2\text{O}$ ) exposures and gypseous soils occupy over 100 million ha worldwide, primarily in arid and semiarid regions, with particularly large areas of surface gypsum in southwestern Asia, the Mediterranean region, the Horn of Africa and southwestern North America. Each of these areas hosts a diverse assemblage of gypsum endemic plant taxa, known as gypsophiles. Although plant biologists have been interested in the causes of gypsophily for well over a century, it has only been over the past few decades that gypsophile floras have received sustained ecological and evolutionary study. Recent work, principally in Spain, has revealed that both physical (*e.g.*, gypsum crusts, soil porosity) and chemical (*e.g.*, high Ca and S, low cation exchange capacity) factors may control community structure on highly gypseous substrates. Plant-fungal interactions may also play a key role in plant establishment on gypsum, although few studies have examined this subject. Molecular systematic and population genetic studies over the past two decades have revealed several key similarities in the assembly and evolution of gypsophile floras and taxa. These studies imply that gypsophile lineages have frequently appeared multiple times within clades that are ancestrally tolerant of gypsum, that speciation has been common in the most widespread lineages of gypsophiles, and that most gypsophile lineages first appeared no earlier than the latest Miocene. Population genetic studies have revealed generally higher levels of among-population genetic differentiation and isolation-by-distance within gypsophile taxa, in line with expectations for taxa that are restricted to substrate archipelagoes such as gypsum. Despite these advances in our understanding of gypsophily, gypsum floras remain much more poorly studied compared to other important

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edaphic endemic communities, such as serpentine and halophilic floras, highlighting the need for additional work.

## INTRODUCTION

Surface gypsum ( $\text{CaSO}_4 \cdot 2\text{H}_2\text{O}$ ) deposits and gypsisols occur worldwide in arid and semi-arid regions, covering 100-207 million ha worldwide (Eswaran & Gong, 1991; Herrero, 2004; Herrero & Porta, 2000; Verheye & Boyadgiev, 1997). For example, large areas of exposed gypsum characterize parts of the Horn of Africa region (*e.g.*, Ethiopia, Somalia), North Africa (*e.g.*, Tunisia, Algeria), western Asia (*e.g.*, Iran, Iraq, Turkey), Australia, eastern Spain, and the Chihuahuan Desert region of North America (Escudero et al., 2014; Food and Agriculture Organization, 1998; Merlo et al., 2011). In contrast to most NaCl-rich soils, which are mainly concentrated along sea shores or less commonly in interior deserts and endorheic basins (Merlo et al., 2011), gypsum bedrock exists primarily in interior deposits and is derived from ancient, shallow hypersaline lagoons (Mota et al., 2011). Gypsum may also form in hot springs from volcanic vapors (Herrero et al., 2009) and can form pedogenically (Eswaran & Gong, 1991). Although subsurface gypsum deposits occur worldwide, the high solubility of gypsum means that it persists at the surface for evolutionarily meaningful times almost exclusively in arid and semiarid regions (Escudero et al., 2014; Parsons, 1976).

Gypsum outcrops can be relatively pure or may be combined with other salts, such as sodium chloride. Because of its high solubility, bedrock gypsum often becomes intermixed with surrounding soils, creating mosaics of soils with differing gypsum contents. Gypsum soils (or gypsisols) are characterized by gypsum contents  $> 5\%$  and the presence of a gypsic horizon in which gypsum is accumulated (Food and Agriculture Organization, 1990). Gypsum outcrops can have different physical characteristics, as they can be exposed as massive gypsum evaporite bedrock, crystalline selenite, anhydrite, secondary evaporites or even sand dunes (Figure 1). Physical surface crusts commonly contain  $> 25\%$  gypsum (Verheye & Boyadgiev, 1997).

Plants living on gypsum soils show varying degrees of fidelity to gypsum and employ a variety of survival strategies, both of which have been used as bases for ecological classification (*e.g.*, Davis et al., 1986; Duvigneaud & Denaeyer-de Smet, 1968). The vegetation of gypsum soils includes substrate generalist taxa that grow on and off of gypsum, taxa that grow mostly on gypsum, and taxa that are endemic to gypsum. In recent literature, these three groups of taxa have generally been referred to as gypsovags, gypsoclines, and gypsophiles, respectively (Meyer, 1986), although it is important to note that in older literature the word gypsophile had a much more variable meaning, often referring to any species commonly encountered on gypsum, regardless of its overall fidelity to the substrate (*e.g.*, Johnston, 1941; Powell & Turner, 1977). We follow Meyer's definitions for the purposes of this chapter.

Not coincidentally, the regions with the most extensive gypsum outcrops host the largest assemblages of gypsophiles. Particularly species-rich gypsophile floras exist in the Chihuahuan Desert (at least 200 species; *e.g.*, Johnston, 1941; Moore & Jansen, 2007; Powell & Turner, 1977), Somalia and Ethiopia (at least 50 species; Thulin, 1993; 1995; 1999; 2006), Turkey (at least 40 species; *e.g.*, Akpulat & Celik, 2005), and Spain (at least 40 species; Mota et al., 2009; 2011), with smaller gypsophile floras in Iran (*e.g.*, Akhiani, 2004), North Africa (Le Hou  rou, 1969), Australia (Symon, 2007), the Mojave Desert and Intermountain West of the United

States (*e.g.*, Forbis de Queiroz et al., 2012; Meyer, 1986), Cyprus (Hadjikyriakou & Hand, 2011), and Yemen (Petrusson & Thulin, 1996).



Figure 1. Different physical characteristics of gypsum outcrops, as encountered in the Chihuahuan Desert of northern Mexico: A) rocks (Sierra Tlahualilo, Durango); B) crystals (Puerto de Lobos, Chihuahua); C) crusts (Sierra Roque, Chihuahua); D) sand dunes (Bolsón de Cuatro Ciénegas, Coahuila).

With the exception of the gypsum flora of Spain (Mota et al., 2011), gypsophiles have been poorly studied in most areas of the world, especially compared to serpentine and halophilic vegetation. For example, in most of the above regions, but particularly in western Asia and the Horn of Africa, gypsum habitats have been underexplored botanically, and it is likely that many more gypsophile taxa remain to be discovered and described. Even in the relatively well-botanized gypsum areas of Spain and the United States, more than a dozen new gypsophile taxa have been described in the past decade (*e.g.*, Atwood & Welsh, 2005; Erben & Arán, 2005; Sivinski & Howard, 2011). While great strides have been made in understanding the physiological and community ecology of gypsophile floras in Spain over the past 20 years, little or no corresponding research has been conducted in other gypsum environments, many of which have much different climates and/or rainfall regimes compared to Spain. Furthermore, it has only been over the 15 years that researchers have begun to assess the phylogenetic and population-level histories of gypsophiles. The present chapter reviews the current state of knowledge for gypsophile ecology and evolution, and identifies areas where additional research is needed to understand this globally important edaphic community.

## GYPSOPHILE ECOLOGY

For well over a century, plant biologists have sought to understand the ecological controls on gypsum plant communities (*e.g.*, Contejan, 1881; Macchiati, 1888). Historically, ecologists have focused on physical (*e.g.*, Johnston, 1941; Meyer, 1986) and/or chemical (*e.g.*, Boukhris & Lossaint, 1970; Duvigneaud & Denaeyer-de Smet, 1968) causes for gypsophily, although more recent debates on the assembly of gypsophile floras have attempted to discriminate between two reference models: the specialist and refuge models (Escudero et al., 2014; Merlo et al., 1998; Palacio et al., 2007). These models closely link ecology with evolutionary processes and apply to other unusual geological substrates such as serpentine as well (Harrison & Rajakaruna, 2011). Below we review current understanding of the physical and chemical aspects of gypsophile ecology, as well as fungal-plant interactions.

### Physical Soil Factors

Several physical characteristics have been posited to influence plant growth in soils with high gypsum content, including soil crusts, density and porosity, and associated phenomena such as water holding capacity. Among these factors, the crust that characterizes most gypsum soils has received perhaps the most attention as a physical soil attribute controlling gypsum endemism (*e.g.*, Cañadas et al., 2013; Romão & Escudero, 2005). In arid soils in general, traditionally two types of soil crusts, physical and biological, have been differentiated (but see Gil de Carrasco & Ramos, 2011). Reprecipitation of gypsum creates a physical crust in gypsum soils that contributes significantly to the formation of the structure of gypsic horizons (Daniells, 2012). However, gypsum soils are also frequently characterized by cryptogamic crusts that also influence soil chemistry and texture (Anderson et al., 1982; for more on cryptogamic crusts, see the section below). Hence it is not easy to separate the relative effects of physical vs. biotic crusts on germination and seedling establishment in gypsum environments. This is a clear example of how difficult it can be to separate the chemical, physical and biological factors when explaining gypsophily. Moreover, physical crusts are not exclusive to gypsum (*e.g.*, Anderson et al., 1982). A search in SCOPUS (10 April 2014) using the terms "soil crusts" and "arid" produced 388 results. Of these, only 39 included the word "gypsum."

While soil crusts have received the bulk of attention from ecologists, the hard upper soil horizons (gypsic and petrogypsic; Herrero & Porta, 2000) in highly gypseous soils also likely influence community composition. The gypsum content of soils influences porosity and root penetration capacity (Poch, 1998). Although gypsisols contain > 5% gypsum, much higher amounts of gypsum tend to characterize gypsophile floras. For example, Salmerón et al. (2014) found an average gypsum content approaching 60% in soils dominated by the gypsocline *Jurinea pinnata* in Spain, which qualifies such soils as hypergypsic (Herrero, 2004). Unfortunately, as Drohan & Merkler (2009) have noted, gypsum content of gypseous soils is rarely provided in most studies. Although there are not many field data, those that are available show that gypsum is a difficult environment for plant roots (Guerrero-Campo et al., 1999). Several studies, mainly of cultivated plants, have noted that gypsum contents > 25% hinder root development (*e.g.*, Boyadgiev, 1974; Mashali, 1996). Poch (1998) found that roots are seldom found in horizons with gypsum content > 60%, and when that percentage exceeds 80%,

roots only grow through preexisting cracks or faunal channels and will otherwise form a mat above the upper boundary of these horizons. Poch (1998) also notes that gypsum soil pores may be irregular and discontinuous, which would seriously affect root development in plants whose roots are concentrated in shallow, highly gypseous horizons. Poch & Verplancke (1997) showed that gypsum content was positively correlated with penetration resistance, although they note that this alone does not explain the poor growth of roots in hypergypsic soils. Furthermore, the resistance of soil to root penetration may be increased upon drying, which may help explain why the effect of gypsum on plants appears much greater in arid and semiarid climates. Gibbens & Lenz (2001) reported that petrogypsid soils in the Chihuahuan Desert restricted rooting depth of shrubs to less than 1 m and thus contributed to vegetative sparseness. Nevertheless, some gypsophiles have been found to possess relatively deep roots (*e.g.*, Mota et al., 2011), and hence the effects of gypsum content on root penetration may not be universal.

Water holding capacity of gypsum soils is also likely to influence gypsum floras. However, here too, the data are contradictory. Several authors claim that gypsum soils have lower water holding capacity (*e.g.*, Meyer & García-Moya, 1989), whereas others have suggested the opposite (Hiouani, 2006). It has also been observed that gypsum soils are moist at depth even when surrounding soils dry completely (Meyer & García-Moya, 1989), and according to Hiouani (2006), moisture tends to increase as the percentage of gypsum increases. These apparent contradictions may be related to the irregular distribution of water in these soils, especially when their gypsum contents are very high (Food and Agriculture Organization, 1990). In these cases the pores in the gypsum may become plugged by the precipitation of leached gypsum (Poch, 1998), which may cause high mortality in the fine roots and limit their performance. Precipitation of gypsum and calcium carbonate around roots has also been reported to occur as a consequence of high calcium concentrations in the rhizosphere (Hinsinger et al., 2009). Further investigation of gypsum particle size and micromorphology, including their influence on soil matric potential, may reveal additional influences on community structure in gypsum soils.

## Soil Chemistry

Although much of the ecological research into gypsophily recognizes that physical and chemical constraints may exist, chemical factors have largely been treated as secondary and have therefore been underexplored (Escudero et al., 2014; Romão & Escudero, 2005). The fact that many gypsophiles, and particularly those that are regionally dominant, seem to be characterized by certain nutritional or chemical profiles, strongly suggests that unusual soil chemistry of gypseous substrates has influenced the evolution of such taxa. Below we summarize the chemical aspects of gypsum soils that plants typically must contend with, with a focus on how gypsophiles deal with excess levels of calcium and sulfur.

In general, gypsum soils are characterized by alkaline pH, high content of carbonates, the dominance of Ca and Mg ions, low NaCl, and above all, reduced fertility (Salmerón-Sánchez et al., 2014). The pH of the gypsum soils varies between slightly and moderately alkaline (Drohan & Merkler, 2009) and is not very different from other calcareous soils (Salmerón-Sánchez et al., 2014). Gypsum does not significantly increase osmotic potential despite its high contents of certain salts and ions (Herrero et al., 2009). Electrical conductivity of these soils is usually below 3 dS m<sup>-1</sup> (*e.g.*, Herrero et al., 2009; Salmerón-Sánchez et al., 2014). For Spanish

gypsum soils, Gil de Carrasco & Ramos (2011) provide an average value of 2.76 dS m<sup>-1</sup> and Herrero et al. (2009) provide a value of 2.25 dS m<sup>-1</sup>.

Gypsum soils are characterized by their lowered fertility. Highly gypseous soils have very little organic matter and a low cation exchange capacity (CEC). The high pH and high concentrations of Ca promote rapid insolubilization of nutrients released by weathering (Gil de Carrasco & Ramos, 2011), and reduce the availability of key macro- and micronutrients such as Fe, K, Mg, Mn, P and Zn (Boscaiu et al., 2013; Oyonarte et al., 2002).

Plants growing in high Ca environments must also deal with the cytotoxicity of this element. Although Ca is an essential element for numerous biological functions, it is toxic at high concentrations in the cytoplasm (Hawkesford et al., 2012). Physiological mechanisms, such as sequestering Ca within cells or in the apoplast via oxalate crystallization, allow plants growing on calcium-rich soils to avoid this toxicity (e.g., Fink, 1991; Franceschi & Nakata, 2005). Plants tolerant of gypsum soils pose no exception. In their study of gypsovags from White Sands, New Mexico, USA, Borer et al. (2012) found that plants have different strategies that allow them to cope with the Ca excess, including the prevention of Ca uptake, the sequestration of foliar Ca in chemically unavailable forms (calcium oxalate), and the maintenance of foliar Ca in labile forms, which may allow it to be excreted from foliar salt glands. These mechanisms largely coincide with the four strategies that allow plants to deal with excess Ca and S found by Duvigneaud & Denaeyer-de Smet (1968; 1973) and Merlo et al. (1998; 2001) among plants growing on gypsum in Spain: the accumulator, the extruder, the assimilator, and the avoider. The first group includes species that accumulate large amounts of Ca, and often S and Mg; slight foliar succulence is characteristic of many of these plants (e.g., *Gypsophila*, *Ononis tridentata*). The extruders contain species from primarily halophilic lineages that possess secretory glands, including *Frankenia* and some *Limonium* (Kleinkopf & Wallace, 1974). The assimilators include groups with S-rich secondary metabolites, including the many taxa of Brassicales (e.g., the families Brassicaceae, Capparaceae, and Resedaceae) that are found on gypsum around the world (see below), all of which may be physiologically preadapted to gypsum. The avoiders are able to finely control ionic import and hence are able to survive on very poor and oligotrophic soils; Duvigneaud & Denaeyer-de Smet (1968) note that most avoider taxa on gypsum are gypsovags.

Since the seminal work by Duvigneaud & Denaeyer-de Smet (1966), gypsophiles have been viewed in general as Ca, Mg and S accumulators. This pattern is evident in Table 1, which summarizes foliar nutrient concentrations for various gypsophiles, gypsoclines, and gypsovags. Values for Ca concentration in the leaves of most plants typically range from 0.5-2.5% (Jones, 2012; Kalra, 1997; Parsons, 1976). Among Spanish gypsophiles, highly elevated levels of Ca (> 5%) have been found in *Gypsophila struthium*, *G. hispanica*, *Ononis tridentata*, *Frankenia thymifolia*, and *Sedum gypsicola* (Table 1). All of these species have slightly succulent leaves (Merlo et al., 1998; 2001), with the exception of *F. thymifolia*, which is an extruder. Another group of Iberian gypsophiles also exhibit above average values (> 3%) of foliar Ca: *Helianthemum squamatum*, *Lepidium subulatum*, *Herniaria fruticosa*, *Coris hispanica*, and *Santolina viscosa* (Table 1). Two Spanish gypsovags, *Helianthemum syriacum* and *Sedum sediforme*, also have Ca levels above 3%, whereas locally endemic gypsophiles such as *Centaurea hyssopifolia*, *Thymus lacaitae* or *Teucrium turredanum* have lower values (Table 1).

The widely distributed Spanish gypsocline *Jurinea pinnata*, which grows on both gypsum and dolomite, also has relatively low levels of Ca (2.6%), although those values are higher on

gypsum than on dolomites (Table 1). This behavior is very similar to that exhibited by the Iberian gypsovags *Rosmarinus officinalis*, *Linum suffruticosum* or *Salvia lavandulifolia* (Palacio et al., 2007). Although little nutrient data from other gypsophile floras are available, Ca concentrations above 5% were found in the Tunisian gypsoclines *Erodium glaucophyllum*, *Zygophyllum album*, and *Moricandia suffruticosa* (Boukhris & Lossaint, 1970; 1972). No data are available for the large and diverse gypsophile flora of the Chihuahuan Desert region, although almost all regionally dominant gypsophiles in that area have slightly succulent leaves (e.g. gypsophile species of *Dicranocarpus*, *Sartwellia*, *Acleisanthes*, *Nama*, *Tiquilia*, and *Nerisyrenia*), suggesting that these taxa are also likely accumulators.

Many of the gypsophile taxa with elevated Ca concentration in Table 1 also possess elevated S and Mg concentration, although the pattern is less consistent for Mg. For example, the Ca accumulators *Gypsophila struthium*, *G. hispanica*, and *Ononis tridentata* possess the highest known S contents of any plants growing on gypsum, and have elevated Mg concentrations as well (Table 1). Other Spanish gypsophiles, such as *Helianthemum squamatum* and *Lepidium subulatum*, have elevated S but much lower Mg concentrations. In contrast, the narrowly distributed gypsophile *Helianthemum conquense* has relatively low foliar concentrations of Ca, Mg, and S (Table 1).

Palacio et al. (2007) suggest that there are two broad categories of gypsophile species: those that are dominant on gypsum and broadly distributed geographically (the regionally dominant gypsophiles) and those that are narrowly distributed. The former group is composed of taxa that are typically succulent-leaved and often show a remarkable ability to accumulate Ca, Mg, and S, as well as the macronutrients that are scarce in gypsum soils such as N and P (Table 1). Whereas many narrowly distributed gypsophiles like *Helianthemum conquense* seem to behave more like gypsovags in terms of nutrient accumulation, some locally distributed gypsophiles such as *Coris hispanica* and *Santolina viscosa* behave similarly to the “stockpiling” regional dominants (Table 1). Even the gypsovag *Helianthemum syriacum* is difficult to separate from the latter two species based on Ca concentration (Table 1). Although not perfect, the relatively strong correlation between regional dominance, foliar succulence, and the strategy of accumulating certain nutrients suggests a syndrome of common adaptations to gypsum soil chemistry, which deserves much further physiological and ecological study. Indeed, as Merlo et al. (2011) have noted, foliar Ca, Mg, and S concentration, as well as Ca:Mg ratio, seem to be useful parameters for establishing differences in the nutritional behavior of plants growing on gypsum, dolomite, and serpentine.

**Table 1. Community characteristics, succulence, and foliar nutrient content for selected gypsophiles, gypsoclines, and gypsovags. All nutrient values are mean percentages; dashes indicate that values were not available. Taxa in bold are gypsophiles; all other taxa are gypsovags, except for the gypsocline *Jurinea pinnata*. Average values for halophytes are provided at the bottom of the table. Key to references: (1) Drohan & Merkle (2009); (2) Duvigneaud & Denaeyer de Smet (1966); (3) Duvigneaud & Denaeyer de Smet (1968); (4) Escudero et al. (2014); (5) M. Merlo et al. (unpublished); (6) Salmerón-Sánchez et al. (2014)**

Species	Population growing on gypsum?	Taxon dominant on gypsum?	Taxon widespread on gypsum?	Succulent?	Ca	Mg	S	Na	N	P	K	References
<i>Arctomecon californica</i>	yes	?	no	yes	3.83	2.47	0.33	0.29	–	0.06	1.88	[1]
<i>Artemisia herba-alba</i>	yes	no	yes	no	1.20	0.33	0.20	0.04	3.94	0.27	1.45	[4]
<b><i>Centaurea hyssopifolia</i></b>	yes	no	no	no	2.60	0.49	0.80	0.06	4.02	0.27	2.33	[4]
<b><i>Coris hispanica</i></b>	yes	no	no	no	3.72	0.13	–	< 0.10	1.65	0.02	0.68	[5]
<i>Eriogonum corymbosum</i>	yes	?	no	no	0.84	2.47	0.31	0.18	–	0.08	2.27	[1]
<b><i>Frankenia thymifolia</i></b>	yes	yes	yes	no	11.00	1.22	1.15	0.13	2.00	0.10	1.80	[2,3]
<b><i>Frankenia thymifolia</i></b>	yes	yes	yes	no	10.66	0.91	–	0.10	1.50	0.04	0.37	[5]
<b><i>Gypsophila hispanica</i></b>	yes	yes	yes	yes	7.83	2.23	4.99	0.03	1.75	0.10	0.93	[2,3]
<b><i>Gypsophila hispanica</i></b>	yes	yes	yes	yes	7.40	1.21	3.00	0.06	2.49	0.19	1.18	[4]
<b><i>Gypsophila struthium</i></b>	yes	yes	yes	yes	6.13	3.94	3.64	1.33	1.55	1.26	0.68	[2,3]
<b><i>Gypsophila struthium</i></b>	yes	yes	yes	yes	8.17	0.83	–	< 0.10	1.26	0.08	0.80	[5]
<b><i>Helianthemum alypoides</i></b>	yes	yes	no	no	1.83	0.25	–	< 0.10	1.08	0.07	0.28	[5]
<b><i>Helianthemum conquense</i></b>	yes	no	yes	no	1.90	0.26	0.10	0.03	1.68	0.11	0.39	[4]

**Table 1. (Continued)**

Species	Population growing on gypsum?	Taxon dominant on gypsum?	Taxon widespread on gypsum?	Succulent?	Ca	Mg	S	Na	N	P	K	References
<i>Helianthemum squamatum</i>	yes	yes	yes	yes	3.43	0.65	2.90	0.08	1.65	0.12	0.62	[4]
<i>Helianthemum squamatum</i>	yes	yes	yes	yes	3.15	0.78	2.48	0.08	1.37	0.09	0.75	[2,3]
<i>Helianthemum squamatum</i>	yes	yes	yes	yes	2.62	0.42	–	< 0.10	1.14	0.05	0.28	[5]
<i>Helianthemum syriacum</i>	yes	yes	yes	no	3.10	0.50	1.30	0.02	1.10	0.07	0.70	[2,3]
<i>Helianthemum syriacum</i>	yes	yes	yes	no	3.00	0.31	1.00	0.02	1.76	0.11	0.50	[4]
<i>Helianthemum syriacum</i>	yes	yes	yes	no	3.02	0.20	–	< 0.10	1.30	0.08	0.36	[5]
<i>Herniaria fruticosa</i>	yes	no	yes	no	2.90	0.77	1.10	0.05	2.53	0.11	0.92	[4]
<i>Herniaria fruticosa</i>	yes	no	yes	no	3.00	1.30	0.81	0.01	1.00	0.04	0.89	[2,3]
<i>Jurinea pinnata</i> (on dolomite)	no	no	yes	no	2.20	0.71	0.35	0.04	1.47	0.06	1.05	[6]
<i>Jurinea pinnata</i> (on gypsum)	yes	no	yes	no	2.62	0.46	0.51	0.06	2.12	0.04	1.37	[6]
<i>Lepidium subulatum</i>	yes	yes	yes	no	1.80	0.46	2.80	0.02	3.20	0.16	1.40	[2,3]
<i>Lepidium subulatum</i>	yes	yes	yes	no	2.70	0.38	2.30	0.06	5.12	0.25	0.97	[4]
<i>Lepidium subulatum</i>	yes	yes	yes	no	1.83	0.11	–	< 0.10	2.12	0.08	0.36	[5]
<i>Linum suffruticosum</i>	yes	no	yes	no	2.65	2.45	0.06	0.06	2.80	0.17	0.92	[4]
<i>Linum suffruticosum</i>	no	no	yes	no	2.70	0.33	0.08	0.06	2.31	0.14	0.73	[4]
<i>Ononis tridentata</i>	yes	yes	yes	yes	5.57	2.52	6.07	0.03	2.31	0.10	0.68	[2,3]

Species	Population growing on gypsum?	Taxon dominant on gypsum?	Taxon widespread on gypsum?	Succulent?	Ca	Mg	S	Na	N	P	K	References
<b><i>Ononis tridentata</i></b>	yes	yes	yes	yes	5.75	1.84	4.50	0.09	2.42	0.12	0.28	[4]
<b><i>Ononis tridentata</i></b>	yes	yes	yes	yes	4.37	0.86	–	0.20	1.31	0.04	0.24	[5]
<i>Rosmarinus officinalis</i>	yes	no	yes	no	1.15	0.25	0.22	0.04	0.97	0.06	1.29	[2,3]
<i>Rosmarinus officinalis</i>	yes	no	yes	no	1.40	0.28	0.10	0.06	1.09	0.07	0.80	[4]
<i>Rosmarinus officinalis</i>	no	no	yes	no	1.20	0.17	0.10	0.06	1.17	0.09	1.01	[4]
<i>Salvia lavandulifolia</i>	yes	no	yes	no	1.95	0.33	0.10	0.05	1.77	0.10	0.52	[4]
<i>Salvia lavandulifolia</i>	no	no	yes	no	1.50	0.30	0.05	0.05	1.51	0.09	0.58	[4]
<b><i>Santolina viscosa</i></b>	yes	no	no	no	3.01	0.12	–	0.29	1.34	0.06	0.60	[5]
<b><i>Sedum gypsicola</i></b>	yes	no	yes	yes	8.18	0.18	–	< 0.10	2.76	0.05	0.49	[5]
<i>Sedum sediforme</i>	yes	no	yes	yes	4.31	0.10	–	< 0.10	0.69	0.04	0.55	[5]
<i>Teucrium capitatum</i>	yes	no	yes	no	1.90	0.24	0.06	0.04	2.65	0.13	0.72	[4]
<i>Teucrium capitatum</i>	no	no	yes	no	1.80	0.26	0.05	0.05	2.30	0.15	0.63	[4]
<i>Teucrium polium</i>	yes	no	yes	no	2.00	0.61	0.60	0.07	1.67	0.07	0.76	[4]
<b><i>Teucrium turredanum</i></b>	yes	yes	no	no	1.37	0.22	–	< 0.10	0.99	0.03	0.60	[5]
<b><i>Thymus lacaitae</i></b>	yes	no	no	no	1.60	0.40	0.04	0.05	1.42	0.11	0.56	[4]
halophytes (several species)	no	no	yes	yes	1.10	1.64	2.36	9.37	2.28	0.20	1.98	[2,3]

## Fungal-Plant Interactions

Mycorrhizal and endophytic fungal interactions with gypsophiles are poorly understood but may play an important role in structuring gypsophile plant communities. A handful of recent studies have begun to shed light on the community composition of these fungi in gypsum environments. In Spain, Alguacil et al. (2009a; b; 2012) have found an unusually diverse arbuscular mycorrhizal fungus (AMF) community on Spanish gypsum, comparable to that found on non-gypseous sites with much higher plant density. A total of 21 AMF types were found in association with four Spanish gypsophiles: *Gypsophila struthium*, *Teucrium libanitis*, *Helianthemum squamatum*, and *Ononis tridentata* (Alguacil et al., 2009b). As Alguacil et al. (2009a) note, this appears to be the first report of AMF in the genus *Gypsophila* (Wang & Qiu, 2006). Moreover, Alguacil et al. (2009a) found novel AMF sequences among roots of *G. struthium*, suggesting the presence of undescribed species. This new fungal type was found mainly in the less altered gypsum zone, raising the possibility that it could be associated with survival or proliferation of *G. struthium* on gypsum, which could be among the factors underlying the great colonizing power that this species exhibits in abandoned gypsum quarries, where it becomes almost monospecific (Mota et al., 2004). Alguacil et al. (2012) found a higher diversity of AMF in perennial gypsophiles and gypsovags vs. an annual gypsovag, and Porrás-Alfaro et al. (2014) also found that regionally dominant gypsophile taxa in New Mexico have generally higher overall levels of AMF colonization than nearby non-gypseous grasslands. The same authors also found high levels of colonization by dark septate fungi and hyaline septate endophytic fungi.

All of these results accord with the a priori prediction of Palacio et al. (2012) that gypsophiles have a higher degree of mycorrhizal infection than gypsovags, although it is important to note that these authors did not find higher rates of AMF colonization in gypsophiles vs. gypsovags in their own study, nor did they find support for the hypothesis that AMF are responsible for the high levels of soil macronutrients that characterize such taxa. To explain both the high diversity of AMF on gypsophiles and the presence of potentially undescribed taxa, Alguacil et al. (2009a) postulate the existence of strong selective pressures that have been able to promote the specialization of symbiotic microorganisms, helping vascular gypsophiles to proliferate under heavy stress. This hypothesis adds a possible coevolutionary dimension to the mechanisms involved in gypsophily.

## THE ASSEMBLY AND EVOLUTION OF GYPSOPHILE FLORAS

A comparison of existing, albeit incomplete, checklists and other related literature concerning gypsophiles reveals several interesting patterns relevant to the assembly of gypsophile floras worldwide. First, it is clear that each of the major gypsophile floras evolved independently, drawing their constituent taxa from local plant lineages. For example, all of the common gypsophiles in the Chihuahuan Desert (e.g., species of *Tiquilia*, *Acleisanthes*, *Nerisyrenia*, *Nama*, etc.; Figure 2), Spain (e.g., species of *Helianthemum*, *Ononis*, *Teucrium*, *Limonium*, etc.; Figure 3) and Somalia (e.g., species of *Commiphora*, *Euphorbia*, *Kleinia*, etc.) are members of larger genera or species groups with centers of diversity in the same region (Mota et al., 2011; Thulin, 1993; 1995; 1999; 2006; Turner & Powell, 1979). Although some

individual gypsophile taxa may be widely distributed within a particular gypsum region (*e.g.*, *Dicranocarpus parviflorus* in the Chihuahuan Desert), there is no evidence of direct long-distance dispersal of gypsophiles among major gypsum regions, with the possible exception of *Campanula fastigiata*, which is found in both Spain and Cyprus (Hadjikyriakou & Hand, 2011; Mota et al., 2011). Even in larger cosmopolitan genera like *Euphorbia*, *Helianthemum*, and *Campanula*, which have different gypsophiles in multiple major gypsum regions of the world (*e.g.*, gypsophile taxa in *Euphorbia* exist in both Somalia and the Chihuahuan Desert, but these taxa are not shared between the two regions), it is clear based on morphological and/or molecular evidence that the gypsophiles within each genus are locally derived rather than the result of long-distance dispersal (Mota et al., 2011; Thulin, 1993; 1995; 1999; 2006; Turner & Powell, 1979).

A preliminary review of floristic literature also reveals that the overwhelming majority of gypsophiles fall within just a few major flowering plant clades. For example, of 44 Spanish taxa that ranked highest (a rating  $\geq 4$ ) on the lists of gypsum plant taxa from Mota et al. (2009) and Mota et al. (2011), and thus may be considered gypsophiles, 18 are asterids, 9 are Caryophyllales, 6 are Brassicales, and 11 belong to other groups (clade membership *sensu* Angiosperm Phylogeny Group, 2009). Although species lists are incomplete or absent for other regions of the world, patterns of clade membership appear similar to those seen in Spain. The same preponderance of asterids and Caryophyllales characterizes the gypsophile floras of the Chihuahuan Desert, Somalia and Australia, with key Brassicales groups in the former two regions as well [*e.g.*, *Nerisyrenia* (Brassicaceae) in the Chihuahuan Desert, and *Cleome* (Cleomaceae) and *Reseda* (Resedaceae) in Somalia] (Thulin, 1993; Turner & Powell, 1979). For example, 58% of the taxa listed as gypsophiles in Powell & Turner (1977) are asterids and 27% are Caryophyllales, while 9 of the 13 gypsophile taxa listed by Symon (2007) from southern Australia are asterids. This global bias toward clade membership in such groups as asterids, Caryophyllales and Brassicales likely reflects underlying predispositions for gypsum tolerance within these groups. To examine these clade membership patterns more rigorously requires a more thorough global checklist of gypsophiles, which we are currently assembling.

Recent phylogenetic studies that have included gypsophile taxa have also revealed several trends in the origin and evolution of gypsophiles. The overwhelming majority of such studies to date have examined Chihuahuan Desert gypsophiles, with several clear patterns having emerged from these studies. First, multiple origins of gypsophily are typical within plant lineages that appear to be ancestrally tolerant of gypsum. Excellent examples of this phenomenon have been documented in recent studies of regionally dominant gypsophile taxa in the Chihuahuan Desert: Marlowe & Hufford (2007) found three independent origins of gypsophily within *Gaillardia* (Asteraceae), Moore & Jansen (2007) found two origins of gypsophily in *Tiquilia* subg. *Eddyia* (Ehretiaceae), Douglas & Manos (2007) found at least four origins of gypsophily in tribe Nyctagineae (Nyctaginaceae) [although not available to Douglas & Manos (2007), the inclusion of two more gypsophile species of Nyctagineae from Somalia (*Acleisanthes somalensis* and *Commnicarpus reniformis*) raises the number of origins in this clade to at least six (Levin, 2000; M. Thulin, pers. comm.)], McKown et al. (2005) implied at least three origins of gypsophily in subtribe Flaveriinae (Asteraceae), Taylor (2012) found three origins of gypsophily in *Nama* (Hydrophyllaceae) and Schenk (2013)

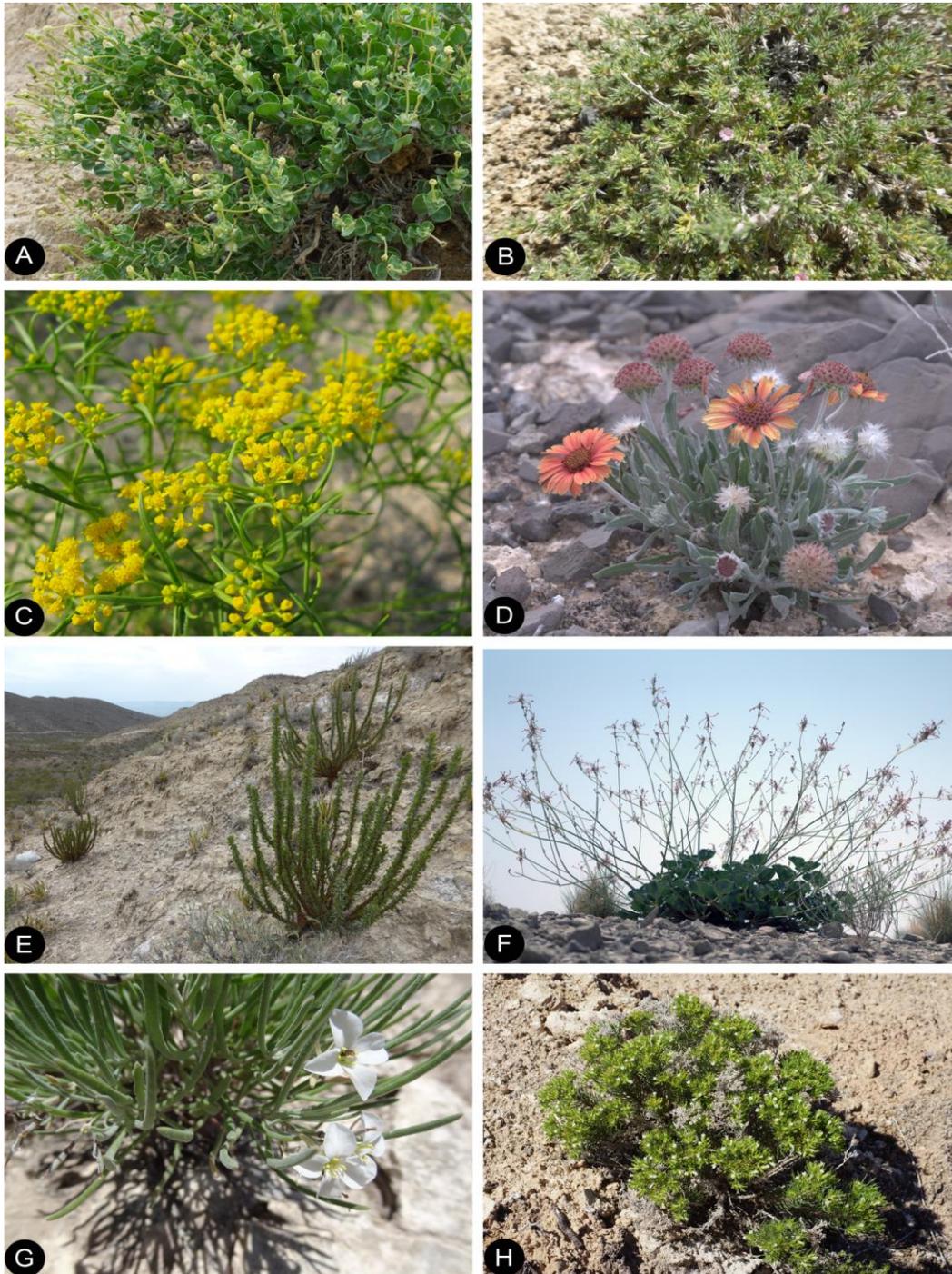


Figure 2. Examples of Chihuahuan Desert gypsophiles: A) *Acleisanthes lanceolata* var. *megaphylla* (Nyctaginaceae); B) *Tiquilia hispidissima* (Ehretiaceae); C) *Sartwellia flaveriae* (Asteraceae); D) *Gaillardia henricksonii* (Asteraceae); E) *Fouquieria shrevei* (Fouquieriaceae); F) *Anulocaulis leiosolenus* var. *howardii* (Nyctaginaceae); G) *Nerisyrenia gracilis* (Brassicaceae); H) *Nama carnosum* (Hydrophyllaceae).

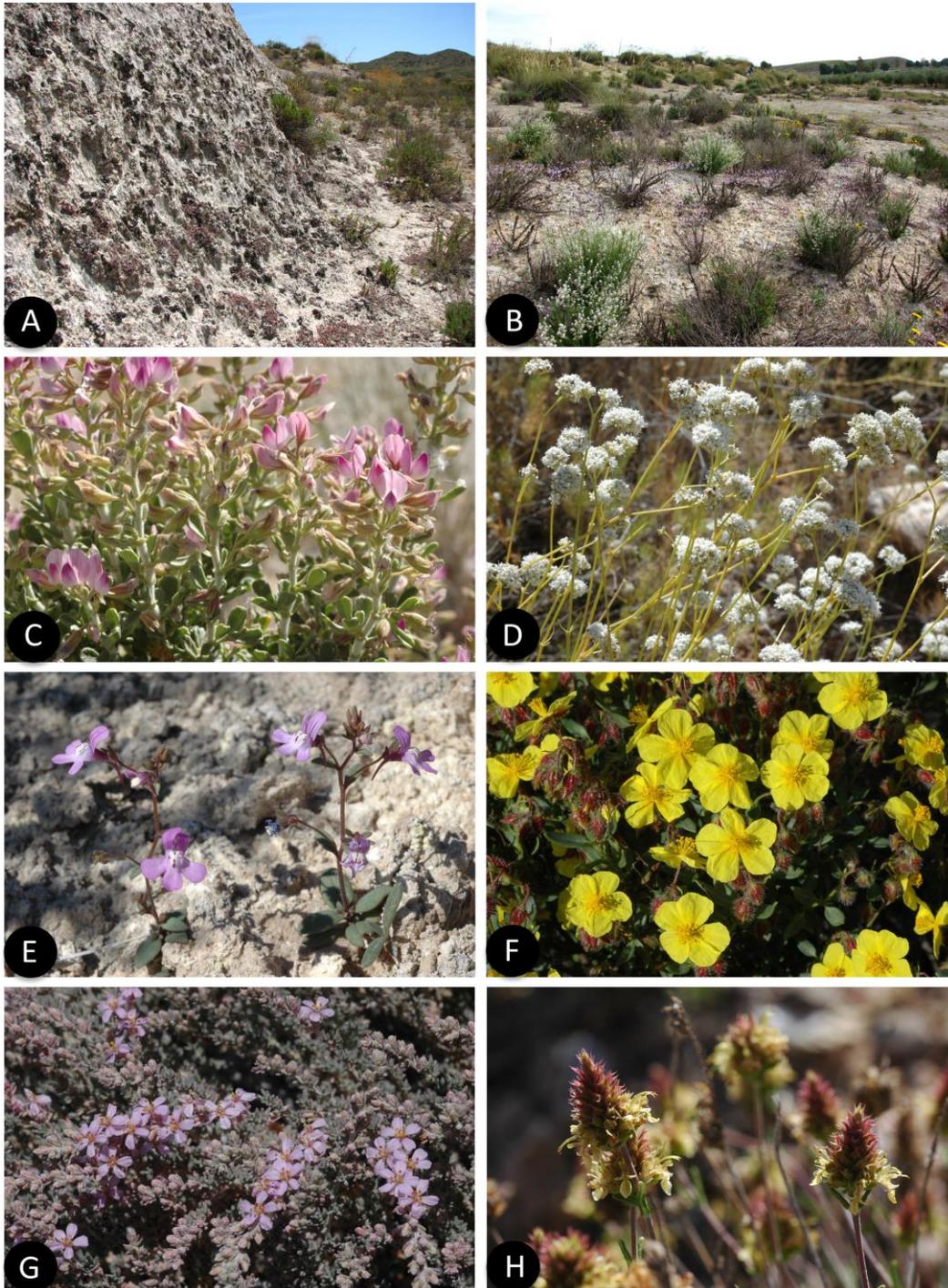


Figure 3. Examples of gypsum habitats and gypsophiles in Spain: A) Gypsum scarp with *Sedum gypsicola* (Crassulaceae) and the lichen *Parmelia pokorny* (Parmeliaceae); B) Gypsum scrubland at Venta de los Yesos, Almería; C) *Ononis tridentata* (Fabaceae); D) *Gypsophila struthium* subsp. *struthium* (Caryophyllaceae); E) *Chaenorhinum grandiflorum* (Plantaginaceae); F) *Helianthemum alypoides* (Cistaceae); G) *Frankenia thymifolia* (Frankeniaceae); H) *Teucrium lepicephalum* (Lamiaceae).

documented up to five origins of gypsophily in *Mentzelia* sect. *Bartonia* (Loasaceae). In all of these examples, the larger group containing the gypsophiles possesses numerous other taxa that are gypsovags. For example, all non-gypsophile taxa in *Tiquilia* subg. *Eddyia* grow both on and off of gypsum (Moore & Jansen, 2007; Richardson, 1977), and numerous members of tribe Nyctagineae (e.g., *Anulocaulis eriosolenus*, all non-gypsophile species of *Allionia* and *Cyphomeris* and many non-gypsophile taxa of *Acleisanthes*, *Boerhavia*, and *Mirabilis*), *Gaillardia* (e.g., *G. pulchella*, *G. spathulata*, and *G. parryi*) and *Mentzelia* (e.g., *M. nuda*, *M. mexicana*, and *M. saxicola*) are also gypsovags (Douglas & Manos, 2007; Schenk, 2013; Thompson & Powell, 1981; Turner & Watson, 2007). Although phylogenetic studies including gypsophiles from other regions of the world are scarcer, those that have been completed support the results from in the Chihuahuan Desert. For example, at least three origins of gypsophily have been confirmed or implied in Spanish *Helianthemum* (Cistaceae; leading to the gypsophiles *H. squamatum*, *H. alypoides*, and *H. conquense*) and Mediterranean *Campanula* (Campanulaceae; leading to the Spanish/Cypriot gypsophile *C. fastigiata*, the North African gypsophile *C. filicaulis* subsp. *reboudiana* and the Turkish gypsophile *C. pinnatifida* var. *germanicopolitana*) and can be expected in Spanish *Limonium* (Plumbaginaceae) (Mota et al., 2009; 2011; Parejo-Farnés et al., 2013; Roquet et al., 2008). Each of these genera is characterized by numerous other gypsovag taxa as well.

Within the gypsophile flora of the Chihuahuan Desert region, existing phylogenetic studies further suggest that speciation has occurred frequently after the acquisition of gypsophily, particularly in those lineages that comprise the regionally dominant taxa on gypsum. Clades of regionally dominant gypsophiles have been documented in phylogenetic studies of *Gaillardia* (which has two gypsophilic clades; Marlowe & Hufford, 2007), *Tiquilia* subg. *Eddyia* (Moore & Jansen, 2007), *Acleisanthes* (Levin, 2000), *Nama* (Taylor, 2012), *Mentzelia* sect. *Bartonia* (Schenk & Hufford, 2011), *Leucophyllum* (Scrophulariaceae; Gándara & Sosa, 2013), and *Argemone* (Papaveraceae; Schwarzbach & Kadereit, 1999), and unpublished data in the senior author's lab suggest that clades of gypsophiles exist in *Sartwellia* (Asteraceae), *Haploësthes* (Asteraceae), *Nerisyrenia* and *Anulocaulis* (Nyctagineae). Although not typically dominant on gypsum, the gypsophile Cactaceae genera *Aztekium* (2 species) and *Geohintonia* (1 species) form a clade and have also speciated on gypsum (Hernández-Hernández et al., 2011). In several of these gypsophile clades, extensive speciation has occurred. For example, the Chihuahuan Desert gypsophile clade of *Acleisanthes* comprises six taxa; the principal clade of *Nama* gypsophiles comprises 10 taxa, of which 8 taxa are gypsophiles; while *Nerisyrenia* is composed almost entirely of gypsophiles, with all but one of 12 described taxa being gypsophiles (Bacon, 1978; Fowler & Turner, 1977; Taylor, 2012). Most of the gypsophile clades, and all such clades with the largest number of taxa, are broadly distributed across the Chihuahuan Desert, despite the island-like nature of gypsum exposures. Although these clades as a whole are broadly distributed, individual taxa within them generally occupy much narrower geographic ranges that are usually allopatric from one another, suggesting that allopatric speciation is typically responsible for taxon boundaries within these gypsophile lineages. A good example of this phenomenon is provided by the gypsophile clade of *Nama*, the distribution of which is illustrated in Figure 4.

While the lack of phylogenetic studies in other gypsophile floras prevents firm conclusions, it is possible that similar phylogenetic and biogeographic patterns may also characterize some of the other more broadly distributed gypsophile floras. For example, possible clades of gypsophiles may exist within *Ononis* (Fabaceae), *Teucrium* (Lamiaceae), *Orobancha*

(Orobanchaceae) and *Chaenorhinum* (Plantaginaceae) in Spain, within *Psephellus* (Asteraceae) in Turkey, and within *Pseudoblepharispermum* (Asteraceae) and *Xylocalyx* (Orobanchaceae) in the Horn of Africa region (Mota et al., 2011; Thulin, 2006; Wagenitz & Kandemir, 2008).

Molecular evidence indicates that many gypsophile lineages around the globe may have appeared no earlier than the late Miocene (*ca.* 8-5.3 mya). Using molecular dating techniques, Moore & Jansen (2006; 2007) found that the two origins of gypsophily in *Tiquilia* subg. *Eddyia* dated most likely to the early Pliocene and early-to-mid Pleistocene, respectively, with the earlier origin leading to the geographically widespread and regionally dominant *T. hispidissima* taxon complex, and the later origin leading to the geographically restricted clade of *T. turneri* and *T. tuberculata*. A late Miocene or early Pliocene divergence time was also favored for the split of the gypsophile (and morphologically quite distinctive) cactus genera *Aztekium* and *Geohintonia* (mean age = 5.67 mya), suggesting gypsophily is at least that old in that lineage (Hernández-Hernández et al., 2014).

In a molecular dating analysis of Cornales (which includes *Mentzelia* of the Loasaceae), Schenk & Hufford (2010) recovered a Pleistocene origin for *Mentzelia* sect. *Bartonia*, which includes numerous gypsophile taxa. Although they did not perform a separate dating analysis of these gypsophile lineages, it is clear from studies with more complete taxon sampling that the regionally dominant and geographically widespread Chihuahuan Desert gypsophile *Mentzelias* (*M. perennis*, *M. todiltoensis*, and *M. humilis*) diverged early in the history of the section, implying that they are older than the other gypsophile taxa of *Mentzelia*, which are all in more recently derived positions, have narrow distributions outside the Chihuahuan Desert, and represent distinct origins of gypsophily (Schenk, 2013; Schenk & Hufford, 2011). Gándara et al. (2014) recovered a late Miocene divergence time between the morphologically distinctive and monotypic gypsophile genus *Jaimehintonia* (Amaryllidaceae) and its nearest relative, suggesting that gypsophily arose in *Jaimehintonia* after that point. Wagstaff & Tate (2011) found a similar late Miocene divergence time between the Australian gypsophile *Lawrencia helmsii* (Malvaceae) and its congeners, again placing a late Miocene upper bound on the origin of gypsophily in this lineage.

In contrast, there are numerous other gypsophile lineages composed of single species that have restricted geographic ranges and are morphologically much more similar to their non-gypsophile relatives. Examples include *Tiquilia turneri*, *Mirabilis nesomii* (Nyctaginaceae), *Abronia nealleyi* (Nyctaginaceae), *Nama stevensii*, and *Gaillardia gypsophila*, all of which have been found to have very little phylogenetic distance separating them from morphologically very similar congeners, implying a very recent origin (Marlowe & Hufford, 2007; Moore & Jansen, 2007; Taylor, 2012; unpublished data). Presumably these taxa appeared in the Pleistocene, as was inferred for *Tiquilia turneri* in the molecular dating analyses of Moore & Jansen (2006; 2007). The existence of a mix of older and younger gypsophile lineages is important because it suggests that modern gypsophile floras have assembled gradually over the last several million years.

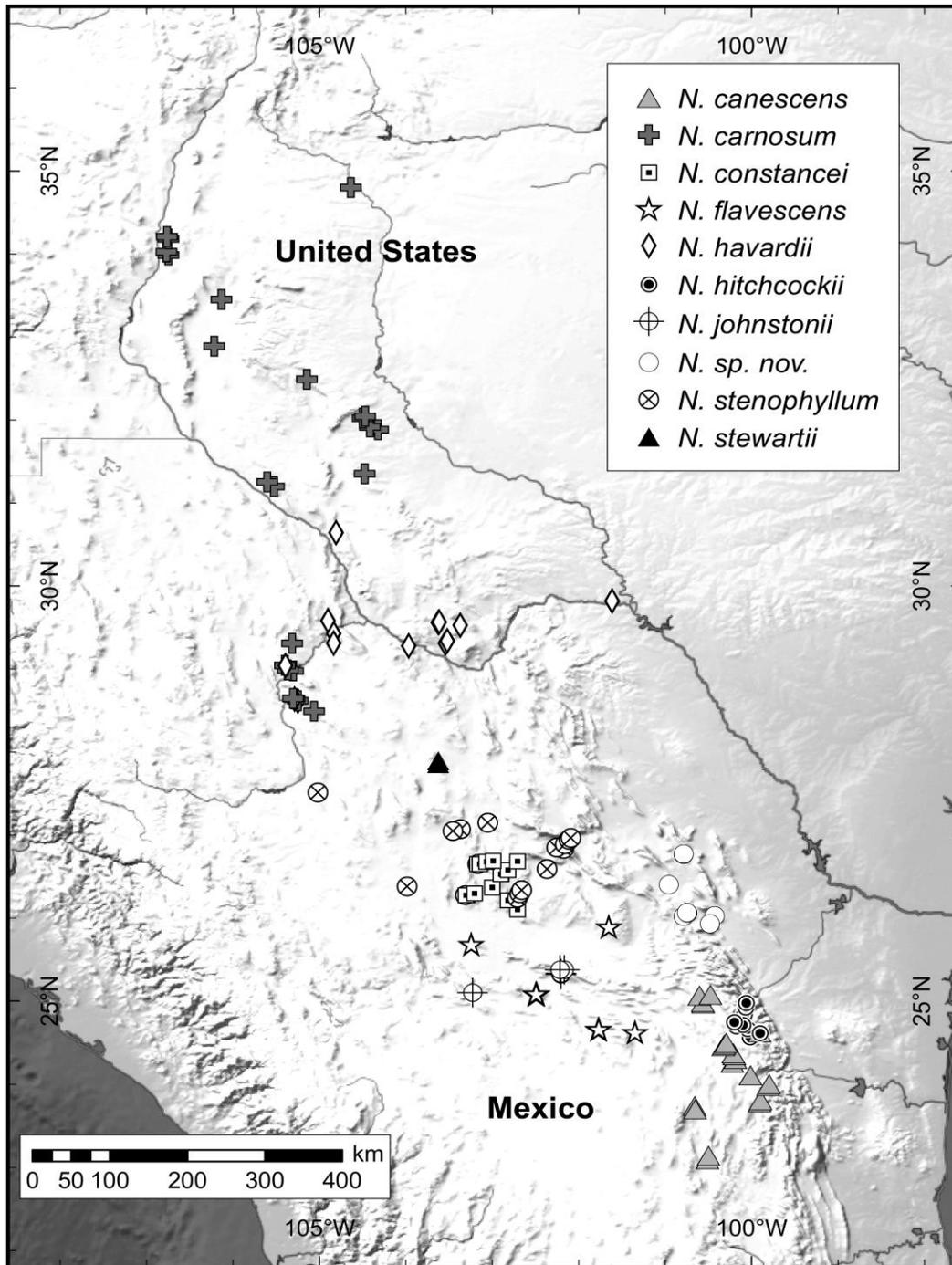


Figure 4. Distribution of taxa within the gypsophile clade of *Nama* (Hydrophyllaceae). All of these taxa are gypsophiles, with the exception of the gypsovags *N. johnstonii* and *N. havardii*.

The post-Miocene assembly of gypsophile floras corresponds well with the current hypotheses concerning the spread of semi-arid and arid habitats during the Cenozoic. After a peak of global average temperature and precipitation in the late Paleocene and early Eocene, the Earth experienced several major episodes of cooling and drying, culminating in the most recent major episode during the latest Miocene and Pliocene (Graham, 2011; Zachos et al., 2008). Available paleoclimatic evidence suggests that it was not until this period that arid and semi-arid regions began to occupy relatively large portions of the Earth's surface (Arakaki et al., 2011; Axelrod, 1979; Graham, 2011; Hernández-Hernández et al., 2014; Salzmann et al., 2008). Given that all of the world's gypsophile plant assemblages occur in such habitats, it is unlikely that gypsum habitats dry enough and extensive enough to support gypsophile floras existed prior to the latest Miocene. Additional molecular dating analyses will be necessary to test this hypothesis further.

## EVOLUTION AT THE POPULATION LEVEL

The population structure of gypsophiles should be largely determined by the island-like distribution of gypsum outcrops across the landscape. This edaphic restriction places an upper limit on the population size any gypsophile species can achieve. Once such a species has colonized a particular gypsum "island," however, it may remain on that outcrop indefinitely. Hence allele frequencies in gypsophiles should reach an equilibrium reflecting the combined effects of migration, mutation and genetic drift. The close correspondence of the island-like distributions of gypsophiles to the assumptions of well-studied theoretical models of population genetic structure (*e.g.*, the stepping-stone model; Kimura & Weiss, 1964) provides an opportunity to infer aspects of their demographic and evolutionary history from parameters commonly estimated in population genetic studies.

In gypsophiles, as with many desert and island taxa (Filner & Shmida, 1981), we would expect migration to be generally quite limited (and selection may actually favor reduced dispersibility; Schenk, 2013). Thus, isolation-by-distance should be evident. While low population size has no effect on mutation rates, at least one aspect of the biology of gypsophiles may serve to increase the effective population size, thus reducing the rate at which genetic diversity is lost due to genetic drift: almost all gypsophiles are perennials, with overlapping generations. Genetic diversity may also be maintained by outcrossing. Only a few gypsophiles are obvious selfers [though mixed mating systems may be common; for example *Acleisanthes* produces both cleistogamous and chasmogamous flowers (Douglas & Manos, 2007)]. On the other hand, biparental inbreeding in small populations may have the opposite effect. Finally, during the climatic oscillations of the Pleistocene, gypsophiles may not have been subjected to repeated genetic bottlenecks as severe as those suffered by plants in other habitats (*e.g.*, alpine taxa), because community composition on unusual substrates such as gypsum may be more stable than substrate generalist communities over a broader range of climates (Damschen et al., 2012; Harrison et al., 2009; Tapper et al., 2014).

In general, endemic taxa tend to have lower genetic diversity than widespread taxa, but measures of population structure do not seem to differ greatly between rare and common species (see reviews by Cole, 2003; Gitzendanner & Soltis, 2000; Hamrick & Godt, 1989).

However, the number of migrants is typically much reduced in rare species (Cole, 2003) as compared to common ones.

To examine whether genetic variation and population structure in gypsophile taxa differ from that in “ordinary” endemics in predictable ways, we followed the example of these three reviews of genetic variation in plants with contrasting life histories (Cole, 2003; Gitzendanner & Soltis, 2000; Hamrick & Godt, 1989). We summarized available estimates of population genetic parameters from five studies that focused on gypsophile taxa; we also included five other studies of Spanish gypsoclines and a study of the gypsovag *Arctomecon californica*, a close congener of the gypsophile *A. humilis*, for comparison (Table 2). We report the following statistics that reflect genetic diversity of these taxa: percentage of polymorphic loci,  $P$ ; number of alleles per locus,  $A$ ; Nei’s total gene diversity,  $H_t$ ; average genetic diversity within populations,  $H_s$ ; effective number of alleles,  $A_e$ ; and observed heterozygosity,  $H_o$ . We also tabulated estimates of population differentiation, including  $G_{st}$ ,  $F_{st}$ , or among-population variance from analysis of molecular variance (AMOVA).

Some studies estimated the effective number of migrants,  $N_m$ . For the sake of comparison, we estimated  $N_m$  from  $F_{st}$  or  $G_{st}$  for the remaining studies where this was possible. Finally, we report the degree to which populations exhibited isolation-by-distance. Averages discussed in the following section exclude diversity parameters estimated from known polyploids, which typically have larger numbers of alleles, and from haploid chloroplast data. Comparisons of parameter values to those obtained from the three reviews should be viewed qualitatively, since the small number of studies of gypsophiles precludes rigorous statistical analysis.

## Genetic Diversity

The taxa in Table 2 tend to show levels of genetic variation similar to that expected for endemic (Hamrick & Godt, 1989) or rare (Cole, 2003; Gitzendanner & Soltis, 2000) plant species, although by some measures, they exceed the genetic diversity typical of widespread species. The percentage of polymorphic loci ranged from 0.10 to 0.82, with a mean of 0.53, intermediate to the averages for rare and widespread taxa in the three reviews cited above. The number of alleles per locus varied from 1.43 to 1.71 (mean 1.59). Though this was reported in only three enzyme studies of diploid taxa, the value lies slightly below averages for rare or endemic taxa in the three reviews. Nei’s total gene diversity ( $H_t$ ) averaged 0.24 (range 0.15-0.34), slightly below the estimated means of endemics in Hamrick & Godt (1989), but actually greater than later estimates for widespread species (Cole, 2003; Gitzendanner & Soltis, 2000). Average genetic diversity within populations is 0.17, slightly higher than found for endemics in general (0.16; Hamrick & Godt, 1989). Perhaps more significantly, the estimated effective number of alleles (Kimura & Crow, 1964), which we estimated as  $1/(1 - H_t)$ , averaged 1.33 (1.18-1.51), while this statistic (which depends on total

**Table 2. Population genetic parameters estimated for gypsophile (in bold) and selected gypsocline species, as well as the gypsovag *Arctomecon californica*. Abbreviations: Pops = number of populations, Inds = number of individuals,  $P$  = proportion of loci that are polymorphic,  $A$  = mean number of alleles per locus,  $H_o$  = observed heterozygosity,  $H_e$  = expected heterozygosity,  $H_t$  = Nei's gene diversity,  $A_e$  = effective number of alleles (calculated from  $H_o$ ),  $H_s$  = mean within-population gene diversity,  $N_m$  = effective number of migrants, IBD = isolation-by-distance. For population differentiation, the following indicators apply: † =  $G_{st}$  or  $F_{st}$ ; ‡ = among-population variance from AMOVA. Average parameter values calculated from diploid data only; # identifies polyploid taxa or haploid genomes excluded from parameter averages. Significant  $R^2$  values identified by an asterisk (\*). The final three entries report parameter averages from published reviews of population parameters in plants, for comparison**

Citation	Taxon	Data Type	Pops	Inds	$P$	$A$	$H_o$	$H_e$	$A_e$	$H_t$	$H_s$	Population Differentiation	$N_m$	$R^2$ (IBD)
Alphin et al., 1998	<b><i>Arctomecon humilis</i></b>	isozyme	6	163	0.104	1.43	0.100	0.103	1.51	0.339		0.620†	0.16	
Hickerson & Wolf, 1998	<i>Arctomecon californica</i>	allozyme	16	480	0.554	1.71	0.158	0.163		0.239	0.163	0.320†	0.54	0.048*
Aguirre-Liguori et al., 2014	<b><i>Fouquieria shrevei</i></b>	cpDNA#	5	94								0.850†, 0.709‡		0.532*
Pérez-Collazos & Catalán, 2008	<b><i>Ferula loscosii</i></b>	allozyme	11	330	0.327	1.62	0.164	0.125	1.18	0.152	0.125	0.134†	1.62	0.839*
Pérez-Collazos et al., 2009	<b><i>Ferula loscosii</i></b>	AFLP	12	342	0.523						0.171	0.440‡	0.32	0.811*
Salmerón-Sánchez et al., 2014	<i>Jurinea pinnata</i>	AFLP	16	160								0.370‡	0.42	
Martínez-Nieto et al., 2013	<b><i>Gypsophila struthium</i></b> subsp. <b><i>hispanica</i></b>	AFLP	7	82	0.573				1.35	0.258	0.200	0.226†, 0.280‡	0.86	0.038
		cpDNA#										0.810		
	<b><i>Gypsophila struthium</i></b> subsp. <b><i>struthium</i></b>	AFLP cpDNA#	16	185	0.562				1.29	0.224	0.160	0.286†, 0.334‡	0.62	0.128
Jiménez & Sánchez-Gómez, 2012	<i>Moricandia moricandioides</i> subsp. <i>pseudofoetida</i>	ISSR	1	50	0.817						0.213	0.533†, 0.665‡	0.19	
	<i>Moricandia moricandioides</i> subsp. <i>moricandioides</i>	ISSR	1	30	0.790						0.213			
Pérez-Collazos et al., 2008	<i>Boleum asperum</i> #	AFLP	10	240	0.913				3.91	0.744		0.202‡	0.99	0.443*

Citation	Taxon	Data Type	Pops	Inds	<i>P</i>	<i>A</i>	<i>H<sub>o</sub></i>	<i>H<sub>e</sub></i>	<i>A<sub>e</sub></i>	<i>H<sub>t</sub></i>	<i>H<sub>s</sub></i>	Population Differentiation	<i>N<sub>m</sub></i>	<i>R</i> <sup>2</sup> (IBD)
Pérez-Collazos & Catalán, 2006	<i>Vella pseudocytisus</i> subsp. <i>pau</i> <sup>#</sup>	allozyme	6	162	0.636				2.23	0.552		0.200‡	1.00	
		<b>AFLP</b>	<b>6</b>	<b>162</b>	<b>0.625</b>				<b>2.39</b>	<b>0.581</b>		<b>0.219‡</b>	<b>0.89</b>	<b>0.560*</b>
López-Pujol et al., 2004	<i>Thymus loscosii</i> <sup>#</sup>	allozyme	8	257	0.850	3.00	0.472	0.422	1.80	0.444	0.429	0.033†	7.33	
<b>Average</b>					<b>0.531</b>	<b>1.59</b>	<b>0.141</b>	<b>0.130</b>	<b>1.33</b>	<b>0.242</b>	<b>0.169</b>	<b>0.423†, 0.466‡</b>	<b>0.589</b>	<b>0.425</b>
Hamrick & Godt, 1989	<b>Endemic</b>				0.400	1.80		0.096	1.15	0.263	0.163	0.248		
	<b>Widespread</b>				0.589	2.29		0.202	1.31	0.347	0.267	0.210		
Gitzendanner & Soltis, 2000	<b>Endemic</b>				0.367	1.94				0.219		0.206		
	<b>Widespread</b>				0.449	2.23				0.242		0.224		
Cole, 2003	<b>Rare</b>				0.407	1.74	0.100	0.113		0.142		0.212	1.190	
	<b>Common</b>				0.588	2.34	0.139	0.150		0.199		0.198	2.240	

heterozygosity) averaged 1.31 among widespread species in Hamrick & Godt (1989). Thus, while gypsophiles tend to possess fewer alleles per locus than most rare or endemic plant species, they do not show obviously reduced heterozygosity. Finally, in the three studies that reported observed heterozygosity,  $H_o$  averaged 0.14, nearly equal to the figure reported for common taxa in Cole (2003). It is likely that the old ages of these populations, and their long-term stability, have allowed allele frequencies to reach equilibrium.

## Population Differentiation

Measures of population differentiation ( $F_{st}$  or  $G_{st}$ : mean 0.42; or proportion of variation explained by differences between populations from AMOVA: 0.47) were in general higher than those found for rare or common species (Table 2) (Cole, 2003). This is not surprising given the static, island-like distribution of their habitats through time. In *Gypsophila struthium* subsp. *struthium* and *G. s.* subsp. *hispanica* (Martínez-Nieto et al., 2013), chloroplast haplotypes were used in addition to nuclear markers (AFLPs) to estimate population differentiation. The estimated values of among-population chloroplast haplotype differentiation were 0.65 and 0.53 in these two taxa respectively, compared to differentiations of 0.33 and 0.28, as estimated by AMOVA on the AFLP markers. A similarly high value (0.65) was obtained from an AMOVA of chloroplast haplotypes from *Fouquieria shrevei*, the only gypsophile taxon from the Chihuahuan Desert that has been studied at the population level (Aguirre-Liguori et al., 2014). The fact that chloroplast differentiation in *Gypsophila* is roughly twice that of the nuclear genome results from inherent differences in effective population size between genomic compartments, which for chloroplasts in hermaphroditic plants is expected to be  $\frac{1}{2}$  that of nuclear loci (Birky et al., 1989). Interestingly, there is no indication of greater differentiation in chloroplast data as one might expect if seed dispersal were more limited than pollen dispersal, or lesser differentiation, which could indicate additional nuclear gene flow via pollen dispersal. In the absence of nuclear data, there is no way to evaluate this in *Fouquieria shrevei*, but it is important to recognize that seemingly very high population differentiation values for chloroplast data do not necessarily imply that seed dispersal is necessarily more restricted than gene flow through pollen.

## Migration and Isolation-By-Distance

Migration was estimated by some authors (Allphin et al., 1998; Hickerson & Wolf, 1998; López-Pujol et al., 2004; Pérez-Collazos & Catalán, 2006; Pérez-Collazos et al., 2009), who generally based their estimates on the value of  $F_{st}$ . While estimates of the number of effective migrants based on population differentiation must be viewed with extreme caution (Whitlock & McCauley, 1999), for the sake of comparison, we calculated values for the gypsophile species based on the reported among-population variation (Table 2).  $N_m$  values thus obtained averaged only 0.59, much lower than the mean value for rare species in Cole (2003). This may reflect the highly discontinuous nature of gypsum outcrops in Spain, where the majority of these population genetic surveys have been conducted. Additional reports from different areas may shed light on how much the patchiness of gypsum outcrops affects migration.

These studies often examined whether genetic distance was correlated with geographic distance, in other words, whether isolation-by-distance (IBD) was evident in their datasets. A stepping-stone model, in which gene flow is a function of geographic distance, is likely to produce such a pattern if populations are at equilibrium. However, if populations have recently expanded into new areas, such a pattern may not have had time to emerge (Slatkin, 1993). Moderate to strong IBD was manifest up to a distance of 24.8 km in the locally distributed gypsoclines *Vella pseudocytisus* subsp. *pau* (Pérez-Collazos & Catalán, 2006) and *Boleum asperum* (Pérez-Collazos et al., 2008). Isolation-by-distance is also evident in the gypsophiles *Gypsophila struthium* sensu lato (Martínez-Nieto et al., 2013) and *Ferula loscosii* (Pérez-Collazos & Catalán, 2008; Pérez-Collazos et al., 2009), which occur in multiple gypsum areas of Spain. In the Chihuahuan Desert, the regionally dominant gypsophile *Fouquieria shrevei* shows IBD as well (Aguirre-Liguori et al., 2014). IBD in these gypsophiles is obviously driven largely by the geographic separation of discrete populations with limited gene flow between them, rather than genetic structure within continuous habitat. In contrast, IBD appears to be weak within subspecies of *Gypsophila struthium* (Martínez-Nieto et al., 2013) and in the gypsovag *Arctomecon californica* (Hickerson & Wolf, 1998), perhaps limited by sustained high gene flow in comparatively continuous habitat, or by recent population expansion.

### General Phylogeographic Patterns

Few of these studies explicitly test a phylogeographic model; however, Pérez-Collazos et al. (2009) discerned a Pliocene colonization of the Iberian Peninsula from north Africa in *Ferula loscosii*, followed by south-to-north dispersal through the Pleistocene. In *Gypsophila struthium* (Martínez-Nieto et al., 2013), chloroplast data suggest that central and eastern Spain represents the ancestral range, which has expanded, and given rise to *G. struthium* subsp. *hispanica* in eastern and, more recently, northern Spain, specifically the Ebro Valley, which is home to several unique gypsophiles. Finally, Aguirre-Liguori et al. (2014) determined that chloroplast haplotypes in *Fouquieria shrevei* are invariant at low elevation sites in western Coahuila, Mexico, which were inundated during pluvials in the Pleistocene, whereas montane gypsum sites show greater diversity, consistent with longer residence of these populations *in situ*. As the number of phylogeographic investigations of gypsophiles increases, we will be able to better characterize the response of populations to historical climate fluctuations, which is key to understanding the diversification of gypsophile floras.

## CONCLUSION

Although great progress has been made in understanding the ecology, assembly and evolution of gypsophile floras worldwide, much remains to be explored in this major but underappreciated edaphic community. The ecological mechanisms controlling the establishment of gypsophile floras deserve further study, especially with regard to interactions among physical, chemical, and biological factors operating in the rhizosphere. Ecological and floristic studies would be particularly welcome in areas with different climates than Spain, especially in places like the Chihuahuan Desert, Iran, and Somalia, all of which have important

differences in rainfall amounts and seasonality compared to each other and to Spain, and which are likely to yield many additional gypsophile taxa. Finally, further phylogeographic and phylogenetic studies are needed in gypsum environments throughout the world to assess whether island biogeographic patterns are typical of gypsum archipelagoes, both at the community and genetic level, and to confirm whether different gypsophile communities share similar ages and assembly characteristics.

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