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ORIGINAL PAPER

1914–2014: A revised worldwide catalogue of cushion plants 100 years after Hauri and Schröter

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Abstract Cushion plants have long fascinated botanists for their ability to cope with extreme environments in most mountains and arctic regions of the world. One century ago, a first worldwide catalogue of species forming cushions was published by Hauri and Schröter (Bot Jahrb Syst Pflanzengesch Pflanzengeogr 50:618–656, 1914). Here, we defined a simplified typology of cushion plants and updated the worldwide catalogue of cushion species, along with information on their geographic distribution. This compilation was based on available information in floras and catalogues but also in efloras and virtual encyclopedias, which were screened using automated database queries. We established a list of 1,309 cushion-forming species distributed in 272 genera and 63 families of angiosperms. Compact cushions are represented by 678 species, among which 587 species exhibit a hemispherical shape, and 91 species exhibit a flat to mat shape. We found 398 species forming non-compact hemispherical cushions. The list of cushion species has significantly increased since Hauri and Shröter, due to the description of new species, updated regional inventories, and improved access to electronic databases. Uncertainties in the delineation of the cushion life form are discussed, notably for non-compact growth forms. A website has been launched to display the catalogue and enable a collaborative improvement of the database (http://www.cushionplants.eu/). The distribution of the species is presented on the basis of the world geographical scheme for recording plant distributions and global biodiversity information facility data. This catalogue will serve as a reference database for further analyses on the biogeography and evolutionary history of cushion plants and arctico-alpine biotas.

Keywords Cushion plants · Alpine plants · Biogeography · Adaptive convergence · Plant life form · Biodiversity informatics

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Introduction

Amongst the extraordinary diversity of life forms displayed by angiosperms, cushion-forming species have long fascinated botanists and alpine plant aficionados. Cushion plants are known as *plantae pulvinatae* in Latin, *plantes en coussin* (or *coussinet*) in French, *plantas en cojín* or *almohadilla* in Spanish and *piante a cuscinetto* in Italian. They were first associated with the high altitude and cold ecosystems of the Alps (Raunkiær 1934) and their remarkable habitat then puzzled the botanists who travelled to newly investigated mountainous areas, notably the Andes, Patagonia, Tierra del Fuego and New Zeland Alps (Ruiz and Pavón 1798–1802; von Humboldt 1805; Weddel 1857; Reiche 1893; Skottsberg 1909; Weberbauer 1931; Cockayne 1912). These areas host a very high diversity of cushion plants in families absent from Holarctic regions or in families showing no examples of cushion habit in Holarctic regions, e.g., the genera *Azorella* (Apiaceae from the Andes and sub-Antarctic islands), *Petunia, Benthamiella* (Solanaceae from

Patagonia), *Raoulia, Haastia* (Asteraceae from New Zealand). It was thus early noted that cushion plants may dominate subalpine and alpine ecosystems far beyond the European alpine region. In addition, expeditions in the Irano-Turanian floristic region allowed measuring the importance of thorny woody cushions, which are typical of a high degree of climatic continentality and long summer drought (Boissier 1867–1888).

Many studies have focused on the moss campion *Silene acaulis*, a widespread arctic alpine species, as a model species to understand the ecophysiology and the population biology of cushion plants (e.g., Körner 2003; Morris and Doak 1998; Molenda et al. 2012). The cushion form represents an efficient trap for heat and water, with a maximum reduction of losses due to its spherical shape (lowest surface-to-volume ratio). The cushion habit, present in several hundreds of plants belonging to various families and genera, represents a good example of evolutionary convergence across phylogenetically unrelated taxa in various cold and/or dry regions of the world (Körner 2003; Sklenář 2009). Cushion plants have a key role in communities, acting as nurse species, with significantly more plant (and arthropod) species growing within cushions than outside their canopy (for a review, see Reid et al. 2010). Alpine cushion plants have also been recently shown to inhibit the loss of phylogenetic diversity in severe environments: these keystone species act as micro-refugia by facilitating less stress-tolerant lineages (Butterfield et al. 2013), and are also associated with particular communities of bacteria and fungi (Roy et al. 2013). Combined with the extraordinary individual longevity of adult plants (Morris and Doak 1998; Halloy 2002), cushion species may thus be important ecosystem engineers, participating in the long-term stability of high alpine biotic communities (Badano et al. 2006).

The first survey of cushion plants was made by the German botanists Reiche (1893), the author of the first flora of Chile. Nearly 20 years after, Hauri and Schröter (1914) proposed a first typology which distinguished flat cushions ("Flachpolster") from hemispherical cushions ("Kugelpolster"), with different categories: radial-growing ("Radial") or tuft ("Schopf" and "Horst"), solid peat-accumulating ("Voll") or not. The catalogue, which was the major objective of the work, listed 338 cushion species including 200 species of compact radial cushions which were termed "Radialvollkugelpolster". These original numbers have been echoed in a number of recent reports (e.g., Ruffier-Lanche 1964; Arredondo-Núñez et al. 2009; Reid et al. 2010).

The authors pointed out the diversity of families (34) and genera (78) in which cushion species were found and discussed their geographical distribution. It was noted that South America contains 50 % of the 338 species, notably in the Andes, Patagonia and Falkland islands. They also observed that a majority of cushion species were growing in mountains or in sub-Antarctic cold wind deserts, with a much higher number of genera in the Southern hemisphere as compared to the Northern hemisphere. Finally, they proposed the possible role of the cushion growth form as an adaptation to xeric environments.

A major contribution was made by Rauh (1939), who was a former student of the famous plant morphologist Wilhem Troll. Rauh dedicated his Ph.D. thesis to the plants with cushion growth form. His major objective was to document the growth of the many cushion plants from their first development stage, in order to better understand how the cushion was organized and built. Outstanding drawings of representative species and synthetic schemes were included in his reference publication (Rauh 1939). This careful analysis of many plants allowed Rauh to refine the typology of Hauri and Schröter (1914) (Fig. 1). Rauh also established an exhaustive list of species in every category of cushion plants. He listed ca 350 species, including new species in addition to Hauri and Schröter's catalogue.

The description of emblematic compact cushion species such as *Androsace helvetica* (L.) All. (Primulaceae of the Alps) or the giant cushions of *Azorella compacta* Phil. (Apiaceae of the central Andes) and *Raoulia eximia* Hook.f. (Asteraceae of New Zealand mountains, known as "vegetable sheep") suggests that the definition of cushion plants should be rather easy. However, distinguishing cushions from mat-forming plants has often been difficult (Raunkiær 1934; Rauh 1939; Gibson and Hope 1986; Parsons and Gibson 2009). Parsons and Gibson (2009) defined cushion plants as chamaephytes or hemicryptophytes growing singly and taking on a hemispherical ("kugel" in German) or subhemispherical to flat ("flach" in German) shape, due to the close branching of their shoots and their short internodes. The leaves are usually small, which allows the shoots to be very closely compacted and the margins of the shoot canopy normally extend downwards to reach ground level. Cushion plants form a continuum from hard, compact species that accumulate peat within their shoots ("voll") to soft, loose, non-peat-accumulating species ("hohl"). Examples of intermediary growth forms between the various types defined below are common and a few species only occasionally take on a cushion form (Rauh 1939). For example, *Azorella selago* Hook.f. may appear as a dense cushion or as a dense mat (Moore 1983). Along an altitudinal gradient of the high afro-alpine mountains, the Asteraceae *Alchemilla subnivalis* Baker f., *Helichrysum newii* Oliv. & Hiern and *H. gofense* Cufod. can shift from an erect shrub habit to a prostrated cushion habit (Hedberg 1986). Some plants may also appear as solitary rosettes or as cushions, i.e., *Phyllactis rigida* (Ruiz & Pav.) Pers. in the Andes or *Potentilla foersteriana* Lauterb., *P. brassii* Merr. & L.M. Perry in tropical

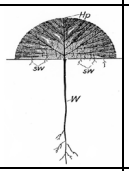
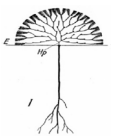
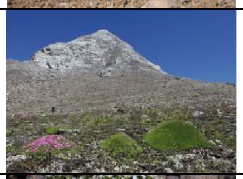
Form	Compactness	Variability	Woodiness	Succulence	Thorniness	Drawing (Rauh 1939)	Example and image	
C	1	0	0	0	0			*Androsace helvetica* (L.) All. (Primulaceae), here in the Alps at ca 2700 m
Herbaceous species with radial compact hemispherical cushion (Rauh's Vollkugelpolster)								
C	0	0	1	0	1			*Onobrychis cornuta* (L.) Desv. (Fabaceae) here at Olang pass , at ca 2200 m, Semnan, Elburz mountains
Woody and thorny species with radial hollow hemispherical cushion (Rauh's Hohlkugelpolster)								
F	1	0	1	0	0			*Silene acaulis* (L.) Jacq. (Caryophyllaceae) here in the Alps at ca 2700 m
Species woody at the base and with radial compact low cushion (Rauh's Vollflachpoolster)								
M	0_1	0	1	0	1			*Arenaria tetraquetra* L. (Caryophyllaceae) here in the Sierra Nevada in Spain at ca 3000 m
Species with woody stock forming a semi-compact creeping cushions (Rauh's Kriechpolster)								
TC	1	0	0	0	0			*Paepalanthus karstenii* Ruhland (Eriocaulaceae), here in the tropical Andes of Venezuela at 3900 m
Herbaceous species forming a tufted compact cushion (Rauh's Rasenpolster)								
C	0	0	1	1	1			*Austrocylindropuntia floccosa* (Salm-Dyck ex Winterfeld) F.Ritter (Cactaceae)
Thorny succulent species forming radial hollow hemispherical cushion(Rauh's Sukkulente polsterpflanzen)								
M or C	1	1	0	0	0			*Azorella selago* Hook.f. (Apiaceae), here in Kerguelen archipelago in communities with *Pringlea antiscorbutica and Festuca magellanica* (left) or as pioneer species (right)
Species woody at the base forming either compact mats (left) or compact hemispherical cushions (right)								
C or 0	0	2	0	0	1			*Phyllactis rigida* (Ruiz & Pav.) Pers. (Valerianaceae) in the Páramo El Angel in Ecuador, at ca 4000 m either as a rosette cushion (left) or solitary (right)
Herbaceous thorny species growing either solitary or forming rosette cushions								

Fig. 1 Examples of cushion plants illustrating various common combinations of the characters described in Table 1 and used to document the catalogue. Pictures by S. Aubert, M. van den Brink, J. Quiles

alpine New Guinea (Mangen 1993; Jorgensen and Ulloa Ulloa 1994).

One century after the landmark study of Hauri and Schröter (1914), we propose to update the catalogue of cushion-forming species, according to the new APGIII nomenclature, and including information on the geographic distribution of each species. To do so, we defined a simplified typology of cushion plants and developed an updated catalogue based on available information in floras and catalogues but also in efloras and virtual encyclopedias, which were screened by the means of semi-automated database queries. A website (http://www.cushionplants.eu) has been launched to display the catalogue and enable a collaborative improvement of this database. The primary

Table 1 Typology of cushions used in the catalogue

Variable	Code	Description	Rauh's types
Form of cushions	C	Hemispherical (dome shaped) cushion	"Radialkugelpolster" (radial hemisphaerical cushions) including "Rosettenpolster-RoP"
	F	Flat cushion	"Radialflachpolster" (radial flat cushions)
	TC	Tufted cushion, densely caespitose	"Rasenpolster-RaP"
	M	Mat, creeping cushion	"Kriechpolster-KP"
	CL	Loose cushion	
	C_M; F_M; C_F; TC_M; C_CL;	Intermediate between the forms described above	
Compactness	1	Compact, hard (peat-accumulating)	"Vollkugelpolster-VKP" and "Vollflachpoolster-VFP" (solid hemispherical and flat cushions, respectively)
	0	Hollow, with canopy gaps	"Hohlkugelpolster-HKP" and "Hohlkugelpolster-HKP" (hollow hemispherical and flat cushions, respectively)
	0_1	Intermediate	
Rauh's types	See above		
variability	0/1/2	No variability/variability/high variability (species with or without cushion habit)	
Woodiness	0/1/2	Herbaceous/woody at base/woody dwarf shrub	
Succulence	0/1	No/yes	"Sukkulentepolster-SP"
Thorniness	0/1	No/yes	
Root system	P/A/R	Single pivotal root/numerous adventitious roots/rhizomes	
Flowers	0/1/2	Flowers sessile/short peduncle/long peduncle	

The typology is derived from Rauh's monograph (1939). For the she shape of the cushions, two major forms are distinguished: hemispherical and flat cushions (most often associated with a radial growth architecture), and two others corresponding to different architectures, i.e., tufted/densely caespitose and mat/creeping cushions. The other variables are the level of compactness and organic matter accumulation within the cushion, the variability of the cushion habit, the levels of woodiness, succulence, thorniness. The root architecture and flower organization were more difficult to document

aim of this work is not to provide a quantitative analysis of cushion species' biogeography and evolution, but rather to detail the elaboration of a catalogue of species with a cushion growth form, which will serve as a basis for future studies about biogeography and evolution of cushion-forming species.

Materials and methods

The typology of cushions

Although sharing major morphological features, cushion plants vary in their vegetative and root architecture. After a detailed analysis of the growth of various species, Rauh (1939) improved the terminology proposed by Hauri and Schröter (1914) and proposed an extensive typology of cushion plants which he used to classify ca. 350 species. This typology has remained as a reference until now, and we initially planned to use it in the present work. However, a precise description of the organization and growth of the plants is not always available and it may vary from one author to the other. Hence, many species were not always easy to assign to a given Rauh's type of cushion. We therefore decided to simplify Rauh's typology and documented several characters, listed in Table 1, which can be used in combinations. The two major criteria used in the present typology are the form of the cushion and its degree of compactness (characters 1 and 2, see Table 1), two parameters usually given by most of the descriptions.

Table 1 lists the traits we considered to elaborate this typology, and Fig. 1 displays characteristic species for different trait combination. As many other authors did we exclude "cushion trees" and "cushion mosses" which were present in Rauh's typology. As different individuals of the same species may vary from one type of cushion to another, we also recorded variability (0 referring to the absence of variability to 2 when the species may appear as solitary rosettes or as cushion). Finally, additional parameters like woodiness, succulentness, thorniness, root system (poorly documented in most of the floras) and the length of the flower or inflorescence peduncle were recorded whenever possible.

Table 2 Main sources of floristic information used to document the catalogue

Continent	Floras, efloras and catalogues
South America	Catalogo de las Plantas Vasculares del Cono Sur (Zuloaga et al. 2008), flora patagonica (Correa 1969–1999), flora of Tierra del Fuego (Moore 1953), flora de Chile (Reiche 1896–1911), eFlora of Chile (2013), catalogue of the vascular plants of Ecuador (Jørgensen and León-Yánez 1999), páramos: a checklist of plant diversity, geographical distribution, and botanical literature (Luteyn 1999), the catalogue of the flowering plants and gymnosperms of Peru (Brako and Zarucchi 1993), flora of Peru (Macbride et al 1936–1971), catalogue of the flowering plants of the Venezuelan páramos (Briceño and Morillo 2002, 2006)
North America	Eflora of North America (2013), USDA Natural Resources Conservation Service (http://plants.usda.gov/java/)
Africa	Hedberg (1964), the Flore de l'Afrique du Nord (Maire 1952–1977), Flore pratique du Maroc (Fennane et al. 1999, 2007)
Europe	Flora europaea (Tutin et al. 1964), flora alpina (Aeschimann et al. 2004), the mountain flora of Greece (Srid 1986–1991), the flora of Turkey and the East Aegean Islands (Davis 1965–1985), the thorny-cushions vegetation in Mediterranean Italy (Nimis 1981)
Asia: Russia, former Soviet republics, China, Pakistan, Mongolia, Irano-Turanian areas	Flora of the USSR (Komarov et al. 1934–1964), key to the vascular plants of Mongolia (Grubov 2001), efloras of North America, China, Pakistan (2013), annotated checklist of the flowering plants of Nepal (2013), Flora Iranica (Rechinger 1963), notably vols. 174–179 (genus *Astragalus*), 108 (Plumbaginaceae)
Australasia	The alpine flora of New Guinea (Van Royen 1982), Gibson and Hope (1986), Gibson and Kirkpatrick (1985), flora of New Zealand (Allan 1961; Moore and Edgar 1976; Healy and Edgar 1980), the student's flora of Tasmania (Curtis 1963–1967; Curtis and Morris 1975–1994), New Zealand alpine plants (Mark and Adams 1995), flora of New South Wales (Harden 1992–2000; eFlora at http://plantnet.rbgsyd.nsw.gov.au), Parsons and Gibson (2009), The NZ Plant Conservation Network (http://www.nzpcn.org.nz/)

When the description of the species included two habits (e.g., mat and cushion), the list refers to a variable morphology (e.g., "mat or hemispherical cushion-forming plant" for *Veronica caespitosa* Boiss. is coded as "C_M").

Elaboration of a cushion species catalogue

We restricted our species catalogue to the sole group of Angiosperms, because extensive data on cushion mosses were not available worldwide. Species were listed as cushions if they were explicitly described as "cushion", "pulvinate", "hummock-forming" or "mounds" or variants (e.g., "tufted to cushion-forming" for *Minuartia juniperina* (L.) Maire & Petitm. in Davis 1967) and combinations of these terms (e.g., "perennial, densely caespitose, cushion-forming" for *Paronychia pulvinata* A. Gray in eFlora of North America). When possible, species described as 'densely tufted' or 'densely caespitose' were analyzed from different sources of literature in order to evaluate if their compactness was sufficient to be considered as cushion-forming species (e.g., "densely caespitose to pulvinate" for *Draba oligosperma* Hook. in eFlora of North America). Finally, species described as 'mats' were only considered as cushion species when mats were characterized as compact or when transitions to hummock or low cushions were described, e.g., "compact mat to hummock-forming subshrub" for the Australian Goodeniaceae *Lechenaultia pulvinaris* C. A. Gardner (encyclopaedia.alpinegardensociety.ne), "densely mat to cushion-forming" for *Minuartia rimarum* (Davis 1967), or "mat to low cushion-forming" for *Werneria aretioides* Wedd. (http://encyclopaedia.alpinegardensociety.net). Nevertheless, the difference between mat-forming and flat cushion-forming species is not easy to delimitate (Foweraker 1917) and would require a detailed analysis of the architecture of the corresponding samples. Our delimitation can be considered arbitrary but is consistent throughout the database; the website displaying the database will be a valuable tool for receiving feedbacks on our morphological classification and improve it over time.

The bases for the establishment of the catalogue were the lists of Hauri and Schröter (1914) and Rauh (1939). In order to be as exhaustive as possible in our listing of cushion species, various sources of information were used including floras, efloras, catalogues, monographs, virtual encyclopedias, and virtual herbaria (listed in Table 2). We used reviews and monographs on certain types of cushions such as cushion bogs (Godley 1978) and on genera comprising cushion species, notably for *Acaena* (Marticorena 2006), *Dionysia* (Lidén 2007), *Abrotanella* (Swenson 1995), *Brayopsis* and *Eudema* (Al-Shehbaz

1990), *Baimashania* (Al-Shehbaz 2000), *Kelleria* and *Drapetes* (Heads 1990), *Azorella, Laretia*, and *Mulinum* (Martínez 1989; Nicolas & Plunkett 2012), *Junellia* (O'Leary et al. 2011), *Opuntia* (Ritz et al. 2012). On the basis on theses monographs, some species of Rauh's list were excluded. For instance, *Azorella biloba* (Schltdl.) Wedd., *A. diversifolia* Clos, and *A. trifoliolata* Clos are not forming cushions according to Martínez (1989) while they were listed as cushion plants by Rauh.

We also used online web resources. The online plant encyclopaedia of the alpine garden society (http://encyclopaedia.alpinegardensociety.net) and the rock garden plants database (http://www.kadel.cz/flora/) were helpful resources, particularly for species growing in regions with no available flora. Whenever possible, these web-resources were compared to professional taxonomic studies, which led to an important reduction in the number of species considered as cushion-forming. We also used the IUCN Red List of Threatened Species (http://www.iucnredlist.org/).

Finally, we implemented automated requests to search for keywords in the species' description of available efloras (http://www.efloras.org/, 2013): North America, China, Pakistan, Chile, and the annotated checklist of the flowering plants of Nepal. A script of automated request. The following keywords were used : "pulvin" (cf. pulvinate, pulvinatus/a, pulvinaris, pulvinatum/a, pulviniformis), "densely tufted", "densely caespitose", "cushion", "hummock", "bolster", "aretioides" (referring to the former name of a section with hard cushions in the genus *Androsace*), "musciformis, muscoides, muscosa, or bryoides" (reference to cushion-moss habit), "azorella, azorelloides, or azorellacea", "oreoboloides", "saxifragoides", and "pycnophylloides" (reference to the cushions in the genera *Azorella, Oreobolus, Saxifraga, and Pycnophyllum*, respectively).

We chose to adopt the nomenclature of the plant list (http://www.theplantlist.org/), the online list of vascular plants developed by the Royal Botanic Gardens, Kew and Missouri Botanical Garden, in collaboration with various contributors. However, the nomenclature of the plant list was not followed with the genus *Convolvulus* which does not include the cushion species. Species' synonyms were consistently checked and the family assignation of each genus was updated according to APGIII (Stevens 2001).

A web catalogue (http://www.cushionplants.eu/) gives access to the full data set including description of cushions, literature sources and worldwide distribution. This opens the possibility for more extensive tests on the sensitivity of the presented results to trait coding. In particular, the difference between hemispherical and flat cushions may be difficult for intermediate shapes. The same problem exists for flat cushions vs. mats.

The geographical data

The distribution of each species has been listed according to the world geographical scheme for recording plant distributions (WGS hereafter, Brummitt 2001). This scheme defines four hierarchical scales, ranging from continents (level 1 with 9 polygons and level 2 with 52 polygons) down to country or province levels (level 3 with 369 polygons and level 4 with 610 polygons). Using all sources of information listed above, we managed to describe the geographic distribution of all species at least at the 3rd level of the WGS for all species. The geographic distribution was documented down to the 4th level of WGS for 85 % of species.

The global biodiversity information facility (GBIF) was also used to complete the geographical distribution of each species. GBIF data were found especially useful to add new level 4-polygons. We checked manually all these new GBIF entries to remove outliers and dubious occurrences. For ca. 250 species, GBIF permitted to increase their described geographic range to neighboring level 4-polygons, as compared to the above-mentioned floras. For example, according to the *Catalogo de las Plantas Vasculares del Cono Sur* (Zuloaga et al. 2008), *Azorella madreporica* Clos grows in Chile (regions III, IV, V, VI, VII) and Argentina (regions Chubut, Mendoza, Neuquén, Río Negro, Santa Cruz, and San Juan). GBIF data permitted to add two neighboring regions of Chile (i.e., region IX and Metropolitan region). Conversely, some mistakes in GBIF data were pointed out and discarded. For instance, *Acantholimon acerosum* (Willd.) Boiss. mainly appeared in Turkey, Armenia, Iraq, Afghanistan and Greece but also with a spot in Canada corresponding to a herbarium specimen. Despite the use of all these sources of information, we acknowledge that the geographical distribution of many cushion plants remains poorly documented. This is particularly true in regions that have been less intensively surveyed by botanists (e.g., Caucasus Mountains) or that are less precisely described by the geographic scheme we used (e.g., Siberia). This is meant to be improved through the development of a participative project, and the possibility of submitting information to the website describing our database (under current development).

Results and discussion

The revised catalogue contains a list of 1,309 species belonging to 273 genera and 62 angiosperm families, including both monocots and eudicots (Table 3). The most frequent categories of cushions accounting for 80 % of the species were: hemispherical shape and non-compact (320 species, 24,4 %); hemispherical shape and compact (236 species, 18 %), hemispherical shape and intermediate

Table 3 Angiosperm families and genera that contain cushion or mat species

Family	Hemispherical cushions		Flat cushions		Other	Genera with cushions or mats
	Compact	Non-compact	Compact	Non-compact		
Acanthaceae	0	1	0	0	0	*Lepidagathis*
Aizoaceae	0	0	0	2	0	*Aloinopsis, Delosperma*
Amaranthaceae	4	3	1	3	0	*Anabasis, Arthrophytum, Hemichroa, Krascheninnikovia, Nanophyton, Ptilotus, Roycea, Sarcocornia*
Apiaceae	24	9	3	3	5	*Aegokeras, Aciphylla, Azorella, Bolax, Bupleurum, Chaerophyllum, Laretia, Mulinum, Trachymene*
Asparagaceae	0	0	0	0	1	*Lomandra*
Asteliaceae	3	0	0	0	0	*Astelia*
Asteraceae	47	25	16	19	19	*Abrotanella, Anaphalis, Anthemis, Argyrotegium, Artemisia, Atractylis, Baccharis, Belloa, Brachyclados, Bryomorphe, Burkartia, Catananche, Celmisia, Centaurea, Chamaechaenactis, Chuquiraga, Cichorium, Dubautia, Erigeron, Euchiton, Euryops, Ewartia, Gamochaeta, Haastia, Helichrysum, Heterotheca, Hippolytia, Jurinella, Lagenocypsela, Launaea, Leontopodium, Leucogenes, Lucilia, Mniodes, Nardophyllum, Nassauvia, Pentacalia, Psephellus, Pterygopappus, Raoulia, Raouliopsis, Saussurea, Scorzonera, Senecio, Sinoleontopodium, Townsendia, Waldheimia, Werneria, Xenophyllum, Youngia*
Boraginaceae	13	6	0	0	1	*Alkanna, Amblynotus, Chionocharis, Eritrichium, Myosotis*
Boryaceae	0	5	0	0	0	*Borya*
Brassicaceae	60	20	4	3	13	*Alyssum, Arabis, Aubrieta, Baimashania, Borodinia, Brayopsis, Dactylocardamum, Degenia, Delpinophytum, Draba, Eudema, Lepidium, Lithodraba, Onuris, Petrocallis, Physaria, Physoptychis, Ptilotrichum, Shangrilaia, Solms-laubachia, Subularia, Thlaspi, Vella, Xerodraba, Zilla*
Bromeliaceae	0	0	0	0	2	*Deuterocohnia*
Cactaceae	0	27	0	0	1	*Austrocylindropuntia, Copiapoa, Cumulopuntia, Echinocereus, Epithelantha, Ferocactus, Gymnocalycium, Maihueniopsis, Mammillaria, Opuntia, Tunilla*
Calceolariaceae	1	1	1	0	2	*Calceolaria*
Campanulaceae	8	0	2	0	2	*Asyneuma, Campanula, Edraianthus, Lysipomia, Muehlbergella, Wahlenbergia*
Caprifoliaceae	7	2	3	3	0	*Aretiastrum, Phyllactis, Pterocephalus, Valeriana*
Caryophyllaceae	77	46	27	1	14	*Acanthophyllum, Arenaria, Bolanthus, Colobanthus, Dianthus, Eremogone, Gypsophila, Minuartia, Mniarum, Paronychia, Philippiella, Pycnophyllopsis, Pycnophyllum, Reicheella, Sagina, Saponaria, Scleranthus, Silene, Stellaria, Thylacospermum*
Celastraceae	0	0	0	0	1	*Stackhousia*
Centrolepidaceae	8	0	0	0	0	*Centrolepis, Gaimardia*
Convolvulaceae	3	1	0	0	3	*Convolvulus*
Crassulaceae	1	0	0	5	0	*Crassula, Sempervivum*
Cyperaceae	16	5	0	0	5	*Carex, Carpha, Oreobolus, Phylloscirpus, Rhynchospora, Schoenus, Zameioscirpus*
Diapensiaceae	1	0	1	0	0	*Diapensia*
Dilleniaceae	0	0	0	4	0	*Hibbertia*
Ericaceae	3	3	1	2	1	*Andersonia, Disterigma, Rhododendron, Dracophyllum, Pentachondra*
Eriocaulaceae	17	0	0	0	1	*Eriocaulon, Paepalanthus*
Euphorbiaceae	1	9	0	0	0	*Euphorbia*
Fabaceae	9	116	0	17	4	*Acacia, Adesmia, Anarthrophyllum, Anthyllis, Astracantha, Astragalus, Carthamus, Chesneya, Cicer, Cousinia, Cytisus, Echinospartum, Erinacea, Eutaxia, Genista, Lotus, Lupinus, Onobrychis, Orophaca, Oxytropis, Sarcopoterium*
Frankeniaceae	0	1	0	2	1	*Frankenia*

Table 3 continued

Family	Hemispherical cushions		Flat cushions		Other	Genera with cushions or mats
	Compact	Non-compact	Compact	Non-compact		
Gentianaceae	2	2	2	0	0	*Gentiana, Gentianella, Halenia*
Geraniaceae	2	1	1	1	1	*Geranium*
Goodeniaceae	2	1	0	0	1	*Lechenaultia, Scaevola*
Iridaceae	1	0	0	0	0	*Tapeinia*
Juncaceae	4	1	0	0	9	*Distichia, Juncus, Luzula, Oxychloe, Patosia*
Lamiaceae	0	2	0	2	2	*Ajuga, Hedeoma, Thymus, Ziziphora*
Linaceae	1	1	0	0	0	*Linum*
Loasaceae	0	1	0	0	0	*Loasa*
Loganiaceae	1	0	0	0	1	*Mitrasacme*
Malvaceae	28	1	0	0	1	*Nototriche*
Montiaceae	2	0	1	0	0	*Hectorella, Lyallia, Phemeranthus*
Oleaceae	0	2	0	0	0	*Jasminum*
Oxalidaceae	4	2	0	0	0	*Oxalis*
Papaveraceae	0	2	0	0	0	*Corydalis*
Plantaginaceae	6	1	7	1	1	*Globularia, Plantago, Veronica*
Plumbaginaceae	14	59	2	3	7	*Acantholimon, Armeria, Limonium*
Poaceae	16	0	0	0	0	*Aciachne, Agrostis, Calamagrostis, Deschampsia, Ehrharta, Kobresia, Poa, Sporobolus, Rytidosperma*
Polemoniaceae	3	2	1	1	1	*Gilia, Phlox*
Polygonaceae	0	1	0	0	1	*Eriogonum*
Portulacaceae	1	0	4	0	0	*Calandrinia*
Primulaceae	62	7	3	0	7	*Androsace, Dionysia, Primula, Vitaliana*
Ranunculaceae	1	0	0	0	3	*Paraquilegia, Psychrophila, Ranunculus*
Rhamnaceae	0	0	0	0	1	*Rhamnus*
Rosaceae	9	6	0	8	4	*Acaena, Ivesia, Petrophytum, Potentilla, Kelseya, Sibbaldia*
Rubiaceae	5	6	3	2	5	*Asperula, Galium, Oldenlandia, Oreopolus, Rubia*
Salicaceae	0	0	0	0	1	*Salix*
Saxifragaceae	97	11	4	4	7	*Saxifraga, Saxifragella*
Scrophulariaceae	0	1	0	0	0	*Verbascum*
Solanaceae	12	0	0	0	5	*Benthamiella, Combera, Fabiana, Pantacantha, Petunia*
Stylidiaceae	3	1	2	0	2	*Donatia, Phyllachne, Stylidium*
Thymelaeaceae	1	2	0	0	4	*Drapetes, Kelleria, Pimelea*
Verbenaceae	5	4	0	4	2	*Junellia*
Violaceae	2	0	2	0	0	*Viola*
Xyridaceae	0	1	0	0	0	*Xyris*
62 families	587	398	91	90	145	273 genera

For 62 angiosperm families, the number of species it contains in the three following types is presented: hemispherical cushions, flat cushions and mats. The last column gives the genera in each family that contain either cushions or mats. In the last row, the total for each category is given. Asteraceae, Caryophyllaceae, Fabaceae and Saxifragaceae stand out as the families that contain the largest numbers of cushion species

compactness (155 species, 12,3 %); flat shape and non-compact (77 species, 5,9 %), tufted cushions and intermediate compactness (72 species, 4,8 %); flat shape and compact (56 species, 4,3 %); tufted cushions and non-compact (49 species, 3,8 %); tufted cushions and compact (41 species, 3,1 %); flat shape and intermediate compactness (30 species, 2,3 %).

Compact cushions represented 678 species, among which 587 species are with a hemispherical shape and 91 species are with a flat shape; 270 thorny species were recorded. These

numbers far exceed the results reported one century ago by Hauri and Schröter (1914), who recorded 200 species of compact hemispherical cushions and 138 other cushions, belonging to 34 families and 78 genera. Families having the highest number of cushion species were Caryophyllaceae (165 sp.), Fabaceae (146 sp.), Asteraceae (126 sp.) and Saxifragaceae (123 sp.) (Table 3).

Many reasons may explain the discrepancy between our catalogue and the one of Hauri and Schröter (1914). First, considerable work of systematics has accumulated around the world since then, leading to the description of many new species, and many species checklists, inventories or catalogues have been published over the last century. Additionally, we multiplied the potential sources of data by using a large number of available floras, efloras, catalogues, and virtual encyclopedias. Second, we may have used a more inclusive definition of cushions. It is clear that, except for the compact (hard) hemispherical cushions, botanists may have diverging ways to consider and classify plant life forms. Therefore, the status of cushion plants usually differs from one flora to the other, according to the various botanists who described them. This is particularly true for non-compact densely tufted cushions with intermediate cases between loosely tufted/tufted/densely tufted/densely tufted cushion-forming. For example, the genus *Leontopodium* is absent in Hauri and Schröter 1914. In Himalayas, according to eFlora of China, this genus has one species among compact hemispherical cushions (*L. haastioides* Hand.-Mazz.), one among compact flat cushions (*L. pusillum* (Beauverd) Hand.-Mazz., present in Rauh 1939), and two species described as "perennial pulvinate herbs" (*L. aurantiacum* Hand.-Mazz. & *L. delavayanum* Hand.-Mazz.). These species were included in our catalogue. Conversely, various species varying from "tufted" to "densely tufted" which have not been integrated as cushion species (eFlora of China). The same holds true for various species of *Townsendia* described as "perennials ± pulvinate" in the eFlora of North America (e.g., *T. hookeri* Beaman), as perennial rosettes in the online plant encyclopaedia of the alpine garden society (http://encyclopaedia.alpinegardensociety.net), and as a cushions in the rock garden plants database (http://www.kadel.cz/flora/). After synthesizing all sources of information, only two species among ca. 10 related species of *Townsendia*, *T. gypsophila* Lowrey & P. J. Knight *and T. hookeri* Beaman, were inserted in our catalogue as non-compact tufted cushions. Similarly, the genus *Asperula* contains various species of non-compact cushions in Greece and Turkey. Ten species of *Asperula* were inserted in our catalogue as hemispherical, flat or tufted cushions while none was listed in Hauri and Schröter (1914) or Rauh (1939). Various other *Asperula* species described as densely caespitose with a tendency to form cushions were excluded from our list.

As a result of these different descriptions of species, the number of non-compact cushions, notably tufted cushions, may therefore be over-estimated in our catalogue. Another source of discrepancy with previous works comes from the two thorny non-compact cushion-forming genera *Astragalus* and *Acantholimon*: the number of species is very high and the status of cushion is not always clear.

The status of some species should be discussed, e.g., the hummock grasses (*Triodia* and *Plechtrachne*), such as pincushion spinifex (*Triodia molesta)* which have not been included, although they might be considered as densely tufted cushions. Similarly, some species listed by Parsons and Gibson (2009) in Western Australia were not listed in our catalogue, on the basis of our criteria. A further limitation is due to the species that may form cushions or not. This species variability is documented in the catalogue. Examples are given with the Valerianaceae *Phyllactis rigida* (Ruiz & Pav.) Pers. (Northern Andes) and with *Potentilla foersteriana* Lauterb. (tropical alpine vegetation in New Guinea), both appearing as solitary rosettes or as a rosette hemispherical cushion.

The 1,309 species of cushion plants are widely distributed in all continents (Fig. 2a; Table 4). Rugged terrains as defined in Korner et al. (2011) show high number of cushions, notably the Andes and the mountains stretching from the Pyrenees to the Himalayas, including the Alps, the Anatolian and the dry Irano-Turanian mountains (Fig. 2a–c). Temperate Asia has the highest number of cushion plants, with 487 species (37.1 % of the total). South America hosts 351 species (26.8 %) including 114 in the cold steppes of Patagonia and Eastern Tierra del Fuego. In terms of number of genera the Andes and Patagonia appear as the richest zones (Fig. 2d). The Southern Alps of New Zealand also appear as an area of high diversity of cushion plants (74 species of the 136 species found in Australasia). Fewer species were observed in North America (87 species), in the Siberian regions, and in the dry mountains of North Africa and Spain. Finally, our results illustrate the difference between different tropical regions: the tropical mountains of Africa indeed contain a low number of cushions (5 species in Eastern Africa and 1 at Mount Cameroun) as compared to New Guinea (39 species) and Ecuador (47 species).

These global patterns have already been reported by Hauri and Schröter (1914) who listed 170 species in South America (50 % of their total), 54 in Asia (16 %), 46 in New Zealand, Kerguelen and Australia (14 %), 40 in Europe (12 %), 10 in Africa (3 %), 9 in the Arctic (3 %) and 8 in North America (2 %) (Table 4). By comparison, our catalogue gives higher number for Asia. This discrepancy may originate from (1) a better knowledge of the South American flora at the beginning of the 20th century, as compared to the Asian flora, notably after the work of Reiche (1893, 1896–1911) and Weberbauer(1931); (2) the numerous species of the genera *Astragalus*, *Astracantha* and *Acantholimon* in Anatolian and the dry Irano-Turanian mountains.

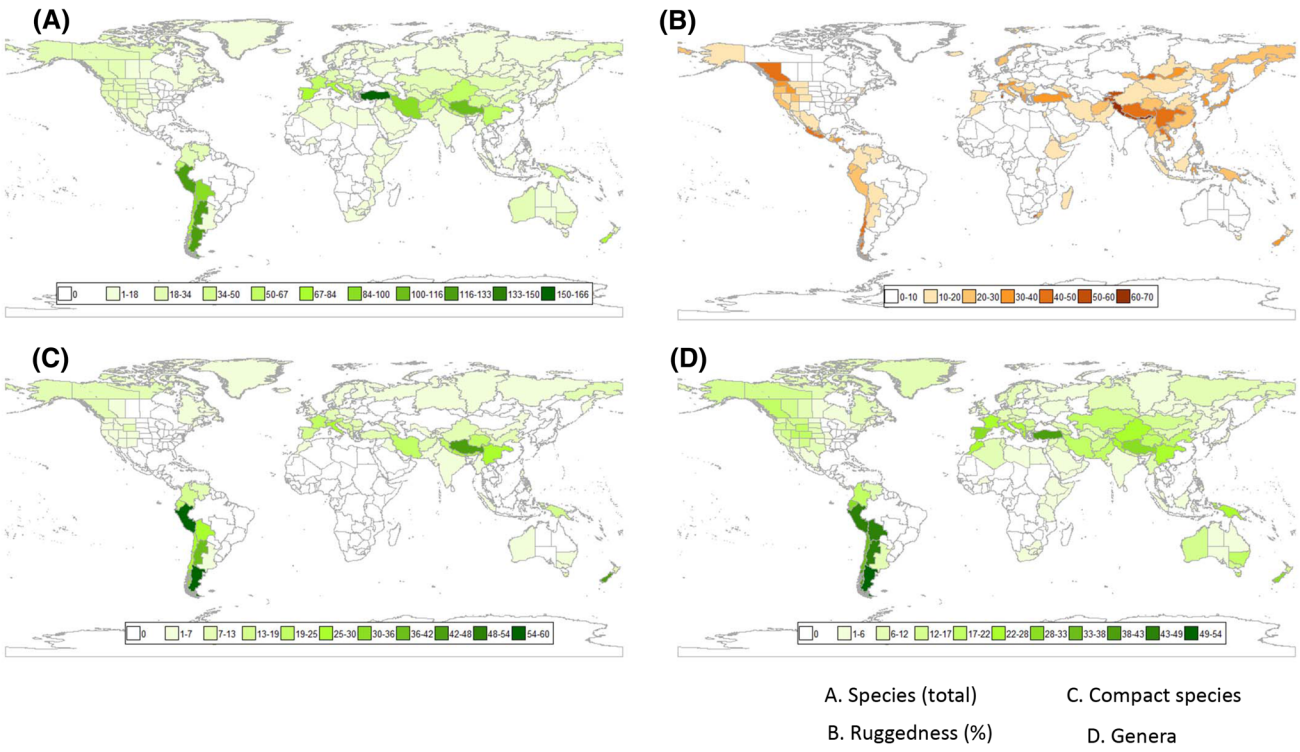


Fig. 2 World distribution of cushion plants on the basis of the level 3 of the world geographical scheme for recording plant distributions (Brummitt 2001). **a** Area of rugged terrain (%, according to Körner 2011); **b** number of cushion species (all life forms); **c** number of cushion species (compact forms only); **d** number of cushion genera (all life forms)

Table 4 Distribution of cushion plants in the continents, on the basis of the world geographical scheme for recording plant distributions (Brummitt 2001)

Continent	Hemispherical cushions		Flat cushions		Other	Total	Proportion of all species in the catalogue (%)
	Compact	Non-compact	Compact	Non-compact			
North America	35	25	8	4	15	87	6.6
South America	166	58	51	28	45	349	26.7
Europe	80	64	17	10	17	188	14.3
Africa	15	26	0	9	6	56	4.3
Asia tropical	76	24	4	6	12	122	9.3
Asia temperate	197	221	10	26	33	487	37.1
Australasia	72	16	6	13	29	136	10.4
Antarctic	8	1	2	0	3	14	1.1

The sum of all proportions exceeds 100 % since some species occur on several continents

A website (http://www.cushionplants.eu) has been launched to display the catalogue and enable a collaborative improvement of this database.

Conclusion and perspectives

To elaborate this worldwide catalogue of cushion plants, we decided to use an inclusive definition of cushion-forming plants. Subsets of the list may be easily produced on the basis of specific characteristics such as compactness or shape (hemispherical vs. flat and mat). We relied on the descriptions available in local floras to document these traits and this may have induced some heterogeneity in information coding. To our knowledge, quantitative measurements of cushion's compactness are missing. There would be an added value to document this plant trait as some authors have pointed out its ecological significance for plant–plant interactions and plant community dynamics (Michalet et al. 2011; Cavieres et al. 2014).

The online catalogue associated with the present work is conceived as an evolving and participative database, and we invite experts to improve this work (suppression/addition of species, revision of the geographic information, images, etc.). It is a contribution to the exploration and explanation of the biological richness of the mountains of the world carried out by the global mountain biodiversity assessment. This database can serve as a basis for inventory and monitoring of these group of species emblematic to arctic and alpine regions. The further analysis of this database will permit to address questions on the evolutionary history of the cushion life form among angiosperms and on the climatic and biogeographic drivers that shape global patterns of cushion plants diversity.

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