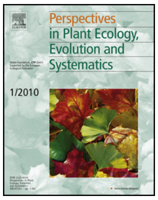
Perspectives in Plant Ecology, Evolution and Systematics 20 (2016) 22–31

Contents lists available at ScienceDirect

Perspectives in Plant Ecology, Evolution and Systematics

journal homepage: www.elsevier.com/locate/ppees



Evolution and biogeography of the cushion life form in angiosperms

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ARTICLE INFO

Article history:
Received 21 October 2015
Received in revised form 15 March 2016
Accepted 18 March 2016
Available online 22 March 2016

Keywords:
Alpine
Angiosperms
Arctic
Biogeography
Cushion plants
Evolutionary convergence

ABSTRACT

Cushion-forming species occur in all cold and dry environments worldwide, where they play important engineering roles. Understanding the origins of cushion plants may thus provide insights into the evolutionary assembly of biomes under extreme climatic conditions. Here we investigate the evolutionary and biogeographic history of cushions in Angiosperms based on a global checklist of all cushion plants, along with phylogenetic, climatic, and biogeographic information. Our aim is to measure the frequency of this evolutionary convergence and to identify its historic, environmental, and biogeographic drivers. We show that cushions appeared at least 115 times in Angiosperms and that they mainly belong to families that occupy the coldest and driest environments on Earth. We found that cushions have intensively diversified in the Himalayas, the Andes, or New Zealand, while other regions like Patagonia have probably been hubs enabling cushion species to migrate between different alpine regions. We conclude that the cushion life form is a remarkable example of convergent key innovation, which has favored the colonization of cold and dry habitats.

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1. Introduction

Cushion plants are emblematic elements of alpine and arctic floras worldwide. Here we consider the cushion as a particular plant life-form characterized by a very dense branching forming a compact canopy. Cushions can be either half-dome shaped or flat (Aubert et al., 2014; see pictures on Fig. 1). Cushion plants are often extremely long-lived organisms, with slow growth rates (e.g. Morris and Doak, 1998; Halloy, 2002). Cushions contain some of the species of angiosperms that occupy the coldest habitats on Earth. Some cushion plants have indeed been recorded above 6000 m in the Himalayas (e.g. members of the genera Arenaria and Stellaria, Grabherr et al., 1995), up to 5200 m in the Andes (e.g. *Azorella compacta*, Halloy, 2002), and above 4200 m in the European Alps (e.g. *Androsace helvetic*a, Werner, 1988), while *Colobanthus quitensis* is one of the few Angiosperms native to the Antarctic continent (Rudolph, 1965). Hundreds of species of cushions exist in many Angiosperm clades and are distributed in all continents (Aubert et al., 2014).

Cushions have long fascinated botanists since the first naturalist explorations of different mountainous regions of the world (e.g. Weddel, 1857; Cockayne, 1912; Hauri and Schröter, 1914). Studies of community ecology have shown that cushion can be keystone species in alpine and arctic environments, where they play an important role as ecosystem engineers (Badano et al., 2006). Indeed, they often act as foundation species that facilitate the establishment of microbes (Roy et al., 2013), of various insects (Molenda et al., 2012; Molina-Montenegro et al., 2006), and of other plant species (Cavieres et al., 2014; Schöb et al., 2012), thereby increasing diversity in alpine environments (Arroyo et al., 2003; Butterfield et al., 2013; Kikvidze et al., 2015).

Given that cushions are important members of arctic and alpine floras, it has long been hypothesized that they are adapted to cold conditions (Raunkiaer, 1934). For example, in the tropical Andes, cushions of *A. compacta* are found in sites where temperature can drop as low as −15 °C and where diurnal variations in temperature can reach 42 °C (Kleier and Rundel, 2009). This has been experimentally confirmed in a study showing that leaves, stems and roots of several cushion species appeared to be resistant to frost

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[1] This paper is dedicated to the memory of Prof. Serge Aubert (1966–2015), a passionate scientist who gave freely of his time and energy to shed light and educate on the biology and evolution of alpine plants.

http://dx.doi.org/10.1016/j.ppees.2016.03.002
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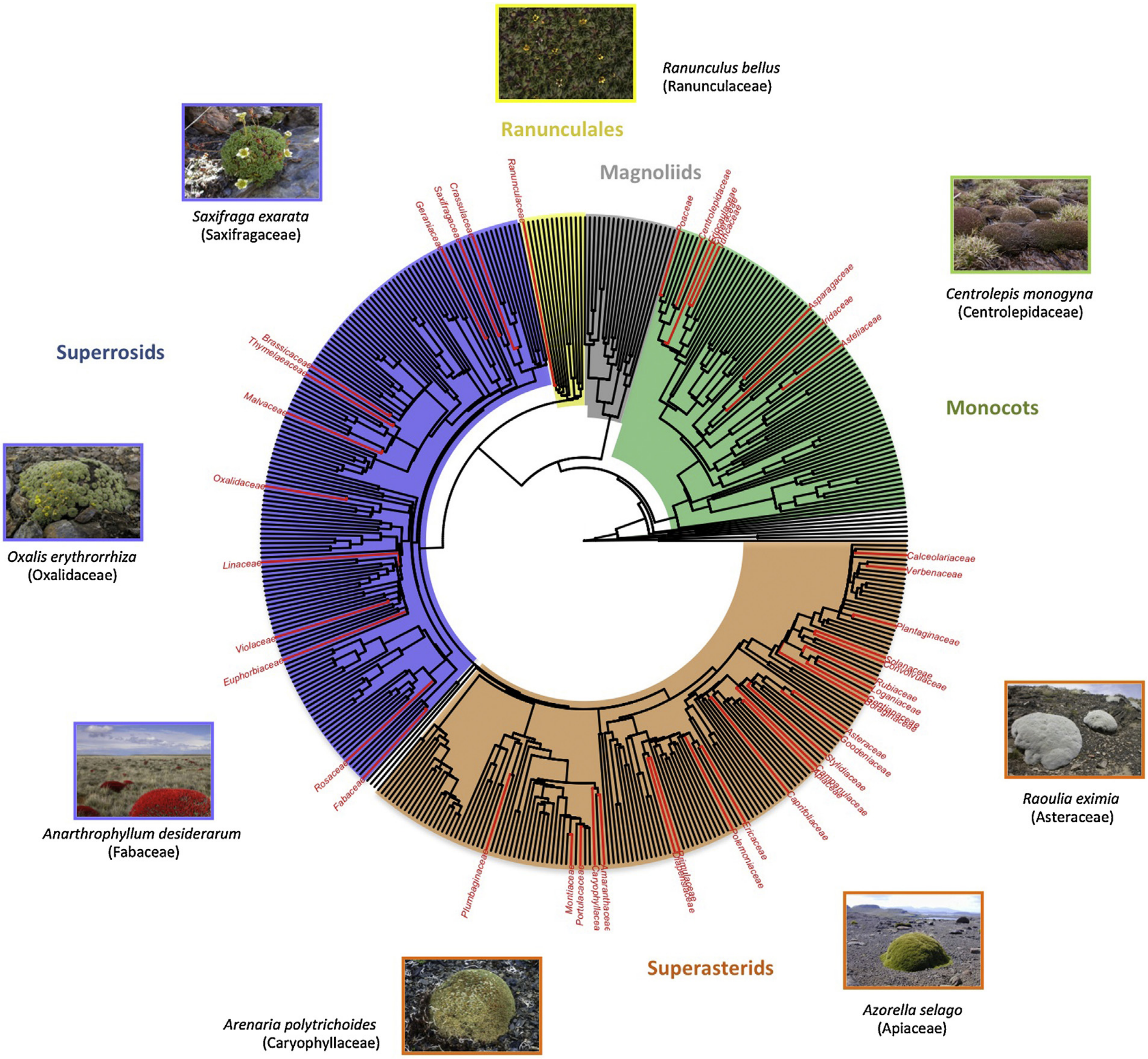

Fig. 1. Distribution of cushion species in Angiosperms. Each tip of this phylogenetic tree is an Angiosperm family (Zanne et al., 2014) and five major groups are underlined with different colors: Monocotyledoneae (green), Magnoliidae (grey), Ranunculales (yellow), Superrosideae (blue), and Superasterideae (orange). Red terminal branches and tips show the 45 families that contain species of compact cushions included in our study. Photographs show a few species of cushions in each major group (taken by S. Aubert, M. van der Brink, F. Danet & R. Hurstel). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

damage up to −15 °C (Larcher et al., 2010). A comparative study of the genus *Androsace* also showed that the evolution of the cushion life-form has allowed the colonization of high alpine climatic niches in this genus (Boucher et al., 2012). However, the cushion life form may also be an adaptation to drought, since the spherical form represents a minimal surface to volume ratio allowing a limitation of water loss (Körner, 1999). Furthermore, it has been suggested that their smooth and dense canopy prevents penetration by cold winds, allowing cushions to limit desiccation (Box, 1981 but see Anthelme et al., 2012 for contrasting results). Some species of cushions indeed inhabit cold deserts, like *Thylacospermum caespitosum*, which is found in places of Eastern Ladakh (*trans*-Himalaya) where precipitation is less than 100 mm/year (De Bello et al., 2011). Importantly, although some level of plasticity exists (Spomer, 1964), the cushion life form is largely inherited genetically (Rauh, 1939).

The cushion life form seems to be a remarkable evolutionary convergence, which emerged in numerous clades of Angiosperms and in different parts of the world (Aubert et al., 2014). This convergence may have happened relatively recently in the history of Angiosperms since alpine and arctic environments, where cushion plants mainly occur, are relatively young (Fine and Ree, 2006),—they have probably appeared after the Eocene climate cooling (Zachos et al., 2001). However, contrary to other key innovations whose evolutionary history is well understood (e.g. C4 photosynthesis, Edwards et al., 2010; Edwards and Smith, 2010), little is known on the evolutionary history of the cushion life form. Indeed, we still do not know the number of independent origins of this life form and whether or not its evolution required precursor traits. In addition, it remains unclear whether the first cushion species appeared in one or a few regions and then spread into most cold and dry habitats on Earth or if they repeatedly evolved from adjacent temperate or tropical floras. These elements all require scrutiny since they would be crucial to understand under which conditions cushion plants evolved, and more generally the history of arctic and alpine floras worldwide.

In this paper we assembled an unprecedented database by combining floristic, phylogenetic, climatic, and geographic information on all known species of co In this paper we assembled an unprecedented database by combining floristic, phylogenetic, climatic, and geographic information on all known species of compact cushions

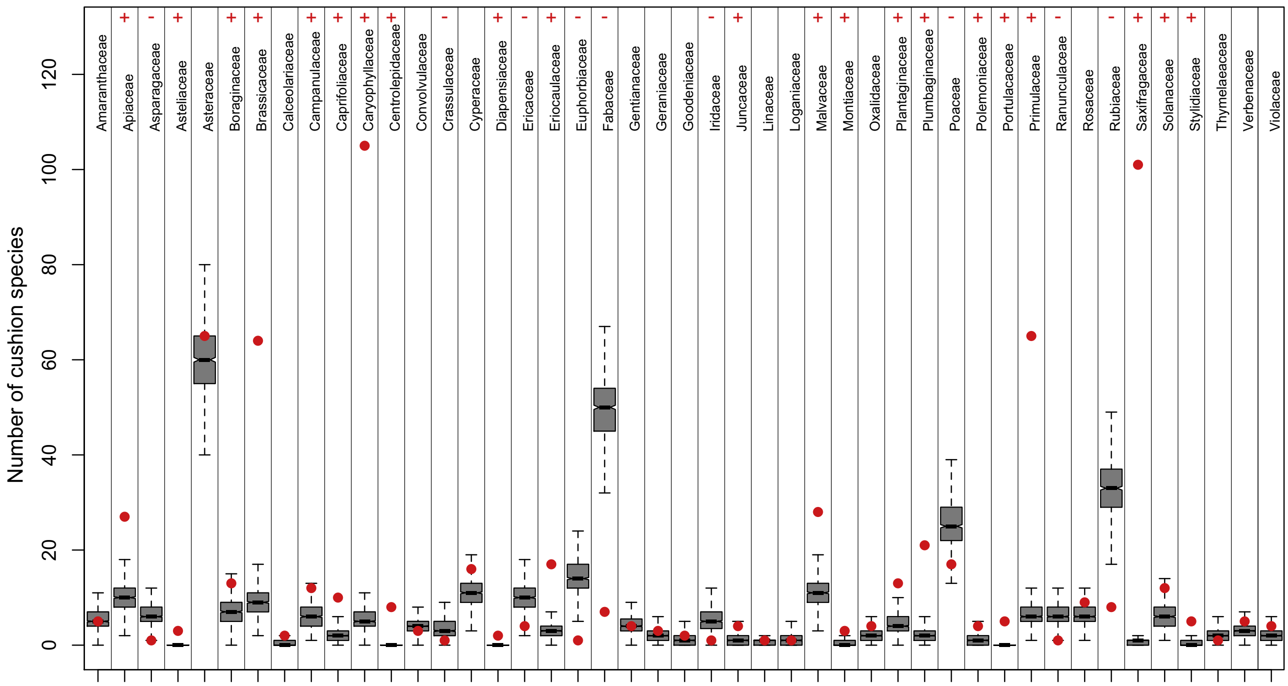

Fig. 2. Number and proportion of cushion species in the 45 Angiosperm families that contain some. For each family, the grey boxplot shows the random distribution of the number of cushions (binomial distribution) while the red dot indicates the actual number of cushions that the family contains. Families marked with a '+' have significantly more cushions species than expected given their richness, while families marked with a '–' have significantly less. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

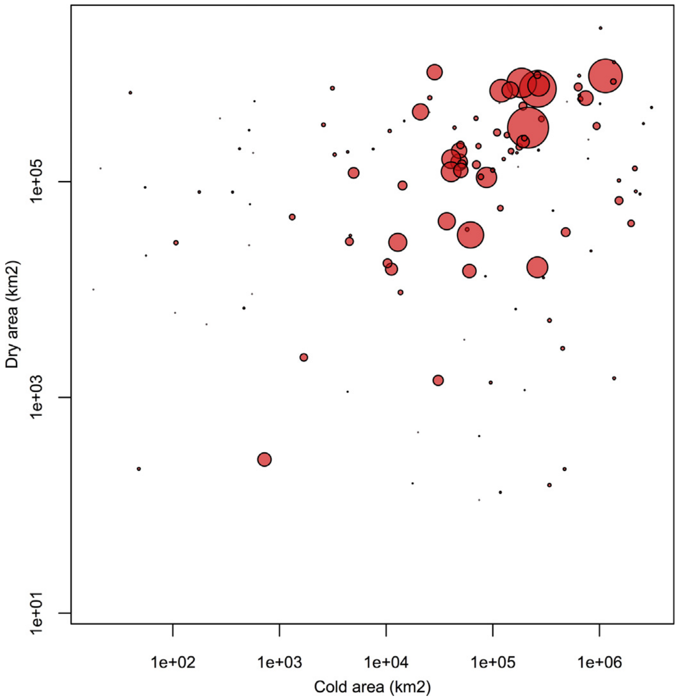

Fig. 3. Biogeographic correlates of the number of cushions in different regions of the world. The x-axis of the plot shows the area of cold environments (*i.e.*GDD < 3000 °C) in each region and the y-axis shows the area of dry environments (*i.e.* AETPET < 0.5). The size of dots is proportional to the number of species of compact cushions in each region. Only the 127 regions of the world that have at least one species of cushion and a strictly positive area of cold and dry environments are represented.

(for definition and a typology of cushions, see Aubert et al., 2014). We use this database to investigate the phylogenetic and biogeographic history of cushion plants, and specifically ask the following questions: (i) how many independent appearances of the cushion life form had there been in Angiosperms?; (ii) did cushions appear at random in different Angiosperm clades or are they disproportionately represented in certain clades?; (iii) has the cushion life form emerged in the angiosperm lineages that have colonized the coldest and/or the driest environments on earth?; and finally (iv) were some regions of the world especially prone to the emergence of cushions while others mostly acted as dispersal routes for cushion species at the global scale?

2. Material and methods

2.1. List of cushion species and phylogenetic relationships

The cushion species inventory used in this analysis has been recently published in Aubert et al. (2014) and is freely available at www.cushionplants.eu. This list of Angiosperm species bearing the cushion life form is the most exhaustive to date and has been compiled using information form various sources including floras, regional checklists, scientific articles and monographs (Aubert et al., 2014 and references therein, plus recent additions listed on www.cushionplants.eu). Information on the morphology of each species is available, including its shape and compactness. The database includes 1327 species that are distributed on all continents in the World and belong to 62 different families of Angiosperms. Family names in this database as well as in this article follow the APGIII nomenclature (The Angiosperm Phylogeny Group, 2009).

From this database we retained the 688 species that have a compact morphology (*i.e.* in which there are no gaps between rosettes), being either dome-shaped (e.g. *Androsace helvetica*) or flat (e.g. *Silene acaulis*). We thus used a conservative definition of cushions, excluding loose cushions (e.g. *Saxifraga oppositifolia*) and mats (e.g. *Raoulia australis*). These cushions belong to 45 different Angiosperm families and 159 genera; they represent 0.25% of all Angiosperm species (c.a. 270,000 species, Vamosi and Vamosi, 2010). They span both monocots and eudicots (see Fig. 1 and list of all species in Table A1). Our choice of including only compact cushions was primarily motivated by the fact that the information on compactness was consistent and almost always given in the sources that were used for building the database. Furthermore, it has been shown that the compact morphology is strongly genetically inherited, whereas it seems to be more plastic in loose cushions or mats (Spomer, 1964).

In order to study the history of the cushion life form in Angiosperms, we used the most detailed phylogeny of Angiosperms to date (Zanne et al., 2014). This tree spans all land plants and includes 30,535 species of Angiosperms (11.3% of all species); it was built using both plastid (*matK, rbcL, atpB,* and *trnL-F*) and nuclear genes (18S, 26S, and ITS) and inferred by maximum likelihood. Divergence times were estimated using 39 fossil calibrations, yielding a crown age of 243.3 Myr for Angiosperms. The age of Angiosperms has been largely discussed in the literature, and this estimate should be interpreted with caution as it is much older than previous estimations (Wikstrom et al., 2001; Davies et al., 2004; Bell et al., 2010; but see Smith et al., 2010). However, in this tree the crown age of eudicots (to which 38 of the 45 families containing compact cushions belong) was estimated to be 136.9 Myr, in agreement with other studies. In this article, all divergence times are given according to Zanne et al. (2014). This species-level tree was then trimmed to build a tree of all 425 Angiosperm families and a tree of 7920 Angiosperm genera (56.4% of all genera, www.theplantlist.org), (hereafter referred to as family-level and genus-level trees, respectively). The family-level tree was used in analyses for which we only had data at the family level (see below). The genus-level tree was used to study the origins of the cushion life form (see below); this latter trimming was necessary since most cushion species studied here were not sampled by Zanne et al. (2014), hence studying the evolution of the cushion life form within genera was not possible.

2.2. Number and proportion of cushion species in families

The number and proportion of species bearing the cushion life form in each family are important to depict the diversity of cushions, but can also provide insights into the history of cushions. Indeed, in families with a low absolute number of cushion species or with a low proportion of species that form cushions, one can hypothesize that the cushion life form has appeared recently or that cushion species diversified relatively slowly. On the opposite, families with a high proportion of cushions may have acquired this character relatively early in their history, leaving time for cushion species to diversify. To tackle this issue, we compared the number of cushion species in each family to the expectation based on the overall frequency of cushion species in Angiosperms, *i.e.* 0.25% (688 spp. out of c.a. 270,000). We thus hypothesized that the expected number of cushions in each family followed a binomial distribution with a number of trials equal to the number of species in the family and a probability of success (*i.e.* of a species being a cushion) equal to 0.25%. The actual number of species in each family was then compared to this binomial distribution to identify exceptionally cushion-rich and exceptionally cushion-poor families.

2.3. Appearing of the cushion life form in angiosperms

To estimate how many times the cushion life form appeared in Angiosperms we used our most detailed phylogenetic hypothesis: the genus-level tree. We coded each genus present in this tree as having at least one species of cushion (1) or not (0) and estimated ancestral values of this binary character using the Mk2 model (Lewis, 2001) with both transition rates being different. Using maximum-likelihood estimates of parameters, we performed 1000 joint reconstructions of this character on the tree and counted the number of independent origins of the cushion life form in each reconstruction. This was done using the packages ape (Paradis et al., 2004) and diversitree (Fitzjohn et al., 2009) implemented in R (R Development Core Team, 2014). Additionally, we also calculated the minimum number of independent origins using parsimony in Mesquite (Maddison and Maddison, 2015).

Importantly, these analyses underestimate the true number of origins of cushions in Angiosperms in two ways. First, the genus-level tree that we used only included 119 out of the 159 genera that contain cushions. Second, our analysis assumes that the cushion life form only appeared once in each genus, which might not be true in some genera.

2.4. Distribution of cushion species in the angiosperm tree

Cushions are widely distributed in the Angiosperm tree (Fig. 1), suggesting that this trait is not too much constrained by the developmental or architectural characteristics of plants. If this life form were randomly distributed among Angiosperms, this would indicate that it is not at all depending on pre-existing biological characteristics in the genera where it occurs. On the contrary, detecting clustering of genera bearing cushions among all Angiosperms would imply that the evolution of the cushion life form depends on pre-existing physiological or developmental features. To test the specific hypothesis that cushions were clustered in particular Angiosperm lineages, we measured mean pairwise phylogenetic distance (MPD, Webb et al., 2002) between genera harboring cushions using the R package picante (Kembel et al., 2010). To provide a null expectation for this index, we used a randomization approach: the index was calculated by drawing 9999 random samples of genera in the tree (same number of genera that those containing cushion species) to build null distributions. The observed MPD values among genera bearing cushions were then compared to the null distributions to test whether genera bearing cushions are clustered (mean distance between two genera bearing cushions smaller than the randomized value) or overdispersed (observed mean distance larger than the randomized one) and to obtain two-sided *P*-values for these tests. This was done first for all angiosperm genera together, and then for specific subgroups

Table 1
Best fitting models for the presence or absence of cushion species in Angiosperm families. The two models with the lowest AICs are presented, with for each term the effect size and the associated p-value between parentheses. The last column gives the value of the parameter describing phylogenetic signal: alpha.

	AIC	Intercept	Dryness	Cold	Dryness:Cold	alpha
Dryness + Cold	162.39	−2.66 (1.69e-10)	−1.11 (1.21e-3)	−1.50 (5.10e-8)	–	0.020
Dryness * Cold	164.55	−2.57 (5.43e-10)	−1.06 (6.41e-3)	−1.46 (7.31e-7)	0.03 (9.29e-1)	0.020

(monocots, Poales, superasterids, and superrosids). As cushions do not appear in the most basal groups of Angiosperms (*i.e.* the *Amborellales*, Nymphaeales, and Austrobaileyales or ANA grade) and because this would increase the randomized values, the genus-level tree was first trimmed to the smallest monophyletic clade containing all cushion species. The phylogenetic distance between two genera was measured as the time since their estimated divergence in the phylogeny of Zanne et al. (2014).

2.5. *Climatic drivers of the evolution of the cushion life form*

To estimate the relative importance of cold and dryness in driving the evolution of the cushion life form, we calculated the climate experienced by a subset of 257 Angiosperm families using worldwide distribution grids at a resolution of 10 arc-minutes provided by the UNEP World Conservation Monitoring Centre (www.unep-wcmc.org). The annual sum of growing-degree days over 5 °C (hereafter GDD5) and the ratio of actual to potential evapotranspiration (hereafter AETPET) were used to capture temperature and water constraints to plant growth and plant distribution at a global scale (Prentice et al., 1992; Stephenson, 1998). We used the Worldclim climate grids (Hijmans et al., 2005) at a 2.5′ resolution to calculate GDD5 as the sum of daily GDD (GDDd) over one year: $\text{GDDd} = \max\{(T_{\max} + T_{\min})/2 - T_{\text{base}}, 0\}$, where $T_{\max}$ and $T_{\min}$ are daily maximum and daily minimum of air temperature respectively, and T_{base} is the baseline temperature that was set to 5 °C here. The ratio AETPET was derived from the MODIS global evapotranspiration products (Mu et al., 2011, 2007). We used the annual total Evapotranspiration and Potential Evapotranspiration to calculate this ratio that was rescaled at a 2.5′ resolution. For each Angiosperm family whose distribution was available, we examined the distribution of GDD5 and AETPET over its range. These distributions were weighted by the area of the different pixels (*i.e.* taking into account that pixels at high latitudes are in reality smaller than pixels at low latitudes). The lower 5% quantiles of these distributions were used to characterize the extremes of each family on the cold and drought gradients.

Finally, we used phylogenetic logistic regression (Ives and Garland, 2010) to study the link between the presence of cushions in a family and its climatic extremes. In this framework, the residuals of the logistic regression are not assumed to be independent but might be correlated due to common ancestry. This phylogenetic signal is measured by the rate of change from one character to the other (presence and absence of cushions in our case), α. Importantly, phylogenetic signal is not assumed *a priori* but its strength is estimated along with model parameters using maximisation of the penalized likelihood, as implemented in the R package phylolm (Ho and Ané, 2014). Since distribution data is not available for Angiosperm genera, we used the family-level tree in this analysis. In this model, the presence of at least one species of cushion in a family was taken as the binary response (*i.e.* cushions or not) using a binomial link. The cold and drought extremes of each family were used as explanatory variables. Given their right-skewed distributions, both variables were first log-transformed. These log-transformed variables were then standardized to a mean of zero and a unit standard deviation in order to be able to compare their effect sizes. Four different models were fitted: two models with a single climatic variable as predictor (cold or drought), one model with the two predictors acting additively, and finally one model with the two predictors acting additively plus their interaction. Models were compared using Akaike's Information Criterion (AIC, Akaike, 1973) and their goodness-of-fit was calculated using Mc Fadden's R-squared corrected for degrees of freedom (Mc Fadden, 1974).

2.6. *Biogeographic patterns of cushion diversity*

We used the World Geographical Scheme for Recording Plant Distributions (Brummit, 2001) to investigate the geographic distribution of cushion plants worldwide. This scheme defines different spatial scales, ranging from continents to countries and provinces. The finest scale that could be documented for all 688 species included in our study was the level 3 classification that divides landmasses of the globe into 369 regions. We acknowledge that the level of precision of this classification is heterogeneous since some regions of the world (e.g. Kazakhstan) are less finely divided than others (e.g. Albania). It is however the most precise that one can achieve on a large sample of plant species and with the species distribution data available for this study. Information on the distribution of every species was initially obtained from the literature and then completed by using Global Biodiversity Information Facility (GBIF, www.gbif.org). Our method thus avoids the shortcoming of being primarily based on the GBIF database, which is notoriously incomplete (see Aubert et al., 2014 for more details).

In order to identify the areas of the globe that contain the highest densities of cushion species, we measured the area of 'cold' environments in each region (*i.e.*GDD5 < 3000 °C, hereafter 'cold area'), as well as the area of 'dry' environments (*i.e.* AETPET < 0.5). These variables were chosen instead of the total area of each region because cushions are primarily found in arctic and alpine regions (see Section 3). The number of cushion species in one region as well as the cold and dry areas of this region was then used to build species-area relationships. Power functions were used to fit these curves, as these are the parametric functions that usually best describe the relationship between species richness and area (Gleason, 1922). We compared four different models using AIC: (i) a model where the number of cushions in each region is a function of the cold area, (ii) a model where it is a function of the dry area, (iii) a model where cold and dry areas act additively on the number of cushions in each region, and (iv) a model where the interaction between cold and dry areas was also included. 'Hotspots' of cushion species were then identified as the largest positive outliers (*i.e.* areas that depart the most from the fitted curve).

Cushion species in a region either result from *in situ* diversification or from immigration from another region. To provide a first look at the historical drivers of the number of cushion species in different regions, we first identified the top 20 hotspots of cushion species, *i.e.* the 20 regions on Earth that contain most cushion species relative to their cold and dry areas. In each of theses hotspots, we calculated the ratio of the number of cushion species to the number of corresponding genera. We expect that regions that have many species of cushions belonging to relatively few genera might have been places where cushions diversified extensively. On the opposite, regions with a relatively high number of genera with cushions but few cushion species might be preferred routes of migration for cushion lineages. We also calculated the proportion of cushion species endemic to each region to estimate a degree of geographic isolation and *in situ* speciation. Finally, we used a similarity-based cluster analysis in order to delineate different biogeographic ensembles of cushion diversity. Floristic dissimilarities between regions were calculated using the binary analogue of the Bray-Curtis distance (Bray and Curtis, 1957), *i.e.* as the number of cushion species present in only one of the two regions divided by the total number of cushion species present in the two regions. For clustering, we used the Partitioning Around Mesoids algorithm (Kaufman and Rousseeuw, 1990), which is a bottom-up clustering technique. The aim of this method is to find the clusters minimizing the sum of dissimilarities within groups. We present results with 11 clusters only since this allows a better visualization and shows the main trends in the distribution of cushion species at the global scale, but also show results for 3, 6, 9 and 20 clusters in Fig. A1 . Clustering analyses were done using the R packages cluster (Maechler et al., 2015) and vegan (Oksanen et al., 2013).

3. Results

3.1. Number and proportion of cushion species in families

The 45 Angiosperm families that contain compact cushions vary widely in their number and proportion of cushion species (Fig. 2). Families containing the most cushion species are Caryophyllaceae (105 spp.), Saxifragaceae (101 spp.), Asteraceae (65 spp.), Primulaceae (65 spp.) and Brassicaceae (64 spp.). On the contrary, only one species of cushion is present in Asparagaceae, Crassulaceae, Euphorbiaceae, Iridaceae, Linaceae, Loganiaceae, Ranunculaceae and Thymeleaceae. However, most cushion-rich families are simply large families, e.g. 23600 spp. in Asteraceae, 3710 spp. in Brassicaceae, 2590 spp. in Primulaceae and 2200 spp. in Caryophyllaceae (Vamosi and Vamosi, 2010). For example, the observed proportion of cushions in Asteraceae and Poaceae falls within random expectations, *i.e.* their proportion of cushion species is similar to one in all angiosperm together (Fig. 2). Nevertheless, Caryophyllaceae, Saxifragaceae, Primulaceae, Brassicaceae, Malvaceae, Plumbaginaceae and Eriocaulaceae had significantly more cushion species than expected under random diversification (Fig. 2). Families containing the highest proportions of cushions are Saxifragaceae (27.3%), Centrolepidaceae (22.9%), Portulacaceae (12.5%), Diapensiaceae (11.1%) and Asteliaceae (8.3%).

3.2. Appearing and distribution of cushion species in the angiosperms tree

The rate of appearing of cushions estimated using the Mk2 model was low (0.0029 origins/Myr, c. 10 times smaller than the rate of origination of genera). On average, we estimated 142.8 independent origins based on the genus-level phylogenetic tree (range: 126–166 over the 1000 different joint reconstructions). This indicates that few pairs of genera share cushion species from a common ancestor. However, this model required that on average 147.3 losses of the cushion life form happened in Angiosperms (range: 80–227). The absolute minimum number of independent origins of the cushion life form in Angiosperms, obtained using parsimony, was 115. In this parsimonious scenario, only the following pairs of genera could have inherited the cushion life form from a common ancestor: *Gaimardia* and *Centrolepis* (Centrolepidaceae), *Saxifraga* and *Saxifragella* (Saxifragaceae), *Hectorella* and *Lyallia* (Montiaceae), *Fabiana* and *Petunia* (Solanaceae).

When examining the distribution of cushions in Angiosperms, we found that there was strong clustering at deep phylogenetic scales, but much less at shallower levels. Genera bearing species of cushions were indeed strongly clustered among Angiosperms ($P = 0.0002$), which largely reflects the fact that the 20 orders containing cushions are themselves clustered among Angiosperm orders ($P = 0.0038$, see Fig. 1). Strong clustering was also detected in monocots ($P = 0.0002$) but this was only due to the fact that 19 out of the 20 monocot genera containing cushions belong to Poales. In Poales however, the distribution of genera containing cushion was random ($P = 0.9092$). Genera containing cushions were also clustered in eudicots ($P = 0.0004$), likely because few basal orders in eudicots contain cushions. Focusing on eudicots, we found that cushions were randomly distributed among both superasterids ($P = 0.7658$) and superrosids ($P = 0.2288$).

3.3. Climatic and biogeographic drivers of the evolution of the cushion life form

The best model for the link between the presence of cushions in one family and its climate extremes was a model with additive effects of low temperature and dry environments (AIC = 162.39, R^2 = 26.8%, Table 1). The second best model included additive effects of cold and dryness along with their interaction (AIC = 164.55, R^2 = 25.8%, Table 1), while both models with single predictors had much higher AICs (AIC_{cold} = 175.42, $AIC_{dryness}$ = 205.54). In the best model, cold had a significant positive effect on the probability of presence of cushions in a family ($P < 1e{-}4$). Dryness also had a significant positive effect ($P = 0.0012$), although with a slightly smaller standardized effect size (Table 1). Phylogenetic signal in the residuals was high (α=0.02 character changes/Myr). Overall, cold seemed to be more important than dryness in explaining the presence of cushions in a family, since it had a higher predictive power (R^2_{cold} = 20.8% and $R^2_{drought}$ = 6.9%).

Similarly, the model that best explained the number of cushion species in each region had both the cold and dry areas of each region as explanatory variables (AIC difference with models including only one variable >3.3). Both the cold and dry areas had a significant positive effect on the number of cushions in each region ($P = 0.0035$, t-value = 2.98 and $P = 0.023$, t-value = 2.30, respectively, see Fig. 3). In both cases, the coefficient of the log-log relationship was 0.10, indicating that the number of cushion species in a region strongly levels off as cold and dry area increase. However, the explanatory power of this model was moderate (R^2 = 11.1%) and some regions with large areas of cold and dry environments contained very few cushion species (e.g. Rocky mountains, arctic regions).

The top 20 hotspots of cushion richness were found in Oceania, South America, Asia, and Europe (Table 2). In these hotspots, the mean number of cushion species per genus ranged from less than two in Central and Southern Chile, Columbia, Bolivia, the Northern island of New Zealand and New Guinea, to more than 3.5 in Nepal and Tibet (Table 2). The median outcome over these 20 hotspots was that 17.5% of their cushion species were endemic (Table 2), but two regions had an exceptional level of endemism: New Guinea (72%) and the Southern island of New Zealand (63%).

At the global level our clustering approach revealed main biogeographic regions that formed clusters of cushion species (Fig. 4, Fig. A1). Among these regions, the most striking pattern was that regions of Northern Europe had a cushion flora more similar to that of Eastern Canada than that of the mountaineous regions of Southern Europe. Distinct clusters were formed by the Himalayas, Central Asia, Southern Asia, Oceania, the Andes (including Patagonia), and Austral Africa. Various regions of Northern Africa clustered with the Arabian Peninsula, Somalia, Pakistan, and India. We also found that Mexico clustered with Antarctica, but this was due to the fact that *Colobanthus quitensis*, which is the only compact cushion found in Antarctica, is also found in several regions of Mexico. Finally, many different regions including Western North-America, parts of Brazil, Siberia, Iran, and Kenya were in the same large cluster (Fig. 4).

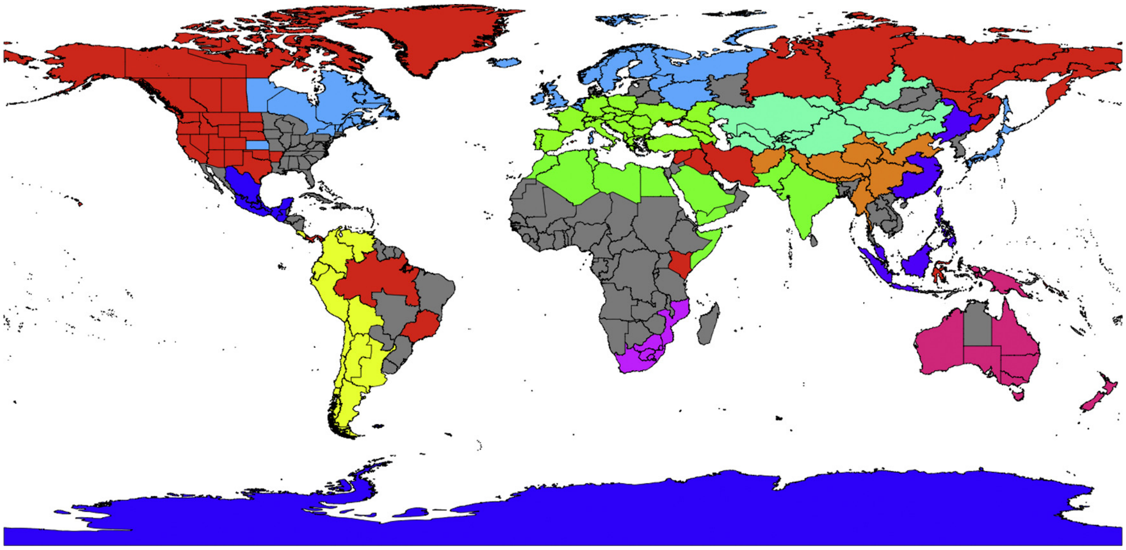

Fig. 4. Main biogeographic regions of cushion diversity. Each color on the map shows the distribution of one of the 11 floristic regions based on a cluster analysis of cushion floras. Each region represents a level 3 area of the World Geographical Scheme for Recording Plant Distributions (Brummit, 2001). Regions plotted in grey do not contain any compact cushion species.

Table 2
Composition of the 20 most cushion-rich regions in the world. Regions are ranked in decreasing order according to the number of species of cushion per area of cold and dry terrain (*i.e.* the first is the hottest hotspot). For each region, the number of species of cushions, as well as the number of genera they belong to, is given. The third column gives the ratio of the number of species to the number of genera of cushions. The last column presents the proportion of cushion species that are endemic to each region.

Region	Species	Genera	Species/Genera	Proportion endemics
New Guinea	29	15	1.93	72%
Peru	89	32	2.78	36%
New Zealand South	57	23	2.48	63%
Argentina South	80	40	2.00	30%
Ecuador	39	19	2.05	26%
Chile South	45	29	1.55	4%
Argentina Northwest	64	28	2.29	8%
Nepal	43	12	3.58	16%
Tibet	73	15	4.87	18%
East Himalaya	37	11	3.36	8%
Chile North	44	22	2.00	2%
Italy	41	12	3.42	15%
Bolivia	49	25	1.96	10%
Colombia	26	14	1.86	8%
Switzerland	22	9	2.44	0%
Chile Central	36	23	1.57	0%
Austria	29	11	2.64	0%
New Zealand North	16	11	1.45	0%
Spain	35	13	2.69	23%
China South-Central	47	15	3.13	11%

4. Discussion

Understanding the evolutionary history of particular morphological adaptations and their relation to specific climatic contexts is an important element of natural history. The evolution and biogeography of the flora of extreme environments has, however, received little attention compared to other regions. In this study, we report on the biogeography and evolution of cushions in Angiosperms using the most comprehensive datasets ever assembled on this plant life form.

4.1. Remarkable evolutionary convergence among angiosperms

The 688 species of compact cushions that we identified belong to 45 Angiosperm families and are found in all major Angiosperm groups except the most early-diverging dicot lineages (Fig. 1). Our most parsimonious estimation yielded a minimum of 115 independent origins of the cushion life form in Angiosperms, and likelihood methods suggest that this number is probably closer to 140 independent origins. This recurrent morphological convergence is remarkable and largely exceeds the number of independent origins of major climate-related plant syndromes, like C4 photosynthesis (*i.e.* 45 origins in Angiosperms, Sage, 2004; 22–24 origins in grasses only, (Christin et al., 2013) or succulence (30 lineages in Angiosperms, Arakaki et al., 2011). This estimate is conservative and the real number of independent origins of the cushion life form may be substantially higher. Indeed, it is likely that the cushion life form evolved repeatedly within some genera. For example, cushions have appeared at least twice in the genus *Androsace* (Boucher et al., 2012) and cushion species are found in different subgenera of the genus Primula (Richards, 2003). If this kind of scenario with multiple origins inside genera were to be the norm rather than the exception, the actual number of origins of the cushion life form could be much higher. Furthermore, the genus-level tree of Angiosperms that we used to infer the history of the cushions life form lacked 40 genera containing cushions. Although some of these missing genera probably do not represent independent origins of cushions, including them into a phylogenetic study of the history of the cushion life form will probably increase the number of detected independent origins.

That the cushion life form is one of the most widespread evolutionary convergences in Angiosperms suggests that selective pressures associated with the emergence of cold and dry biomes (see below) might have been pervasive and strongly directional, provoking the replicated evolution of a similar suite of developmental and physiological features.

Moderate clustering of cushions in Angiosperms suggests few physiological prerequisites – We found that cushions were not randomly distributed among Angiosperm lineages since genera containing cushion species were significantly phylogenetically clustered. This suggests that some physiological or developmental characteristics might be precursors to the emergence of the cushion life form. An obvious character that is needed for the cushion life form to evolve is the presence of ramifications, but this trait alone is unlikely to create the degree of clustering observed since the vast majority of Angiosperm families possess ramifications. The formation of the cushion habit requires dense branching and short internodes. Auxin and cytokine are no doubt important components of these two developmental patterns (Zhao, 2010) and their role in controlling the cushion habit deserves more attention. Moreover, strigolactones have been shown to be inhibitors of branching (Umehara et al., 2008) and some of the genes controlling their synthesis are conserved across large groups of plants (Johnson et al., 2006). However, while they are strongly clustered at deep phylogenetic scales in Angiosperms, genera bearing cushions are randomly distributed within lower-level clades, like Poales, superasteridae, and superrosidae. This suggests that prerequisites for the evolution of the cushion life form might not have been too stringent, making it relatively easy for plants to evolve such a life form when confronted to the strong selective pressures imposed by new alpine or arctic conditions.

4.2. An adaptive convergence to cold and dry environments

Botanists have long recognized that cushions are prominent in alpine and arctic regions around the world (Raunkiaer, 1934) and thus hypothesized that this life-form represents an adaptation to these environments. However, some authors have suggested that the cushion life form might also be an adaptation to the dryness that characterizes many continental mountain ranges (De Bello et al., 2011; Körner, 1999). Using our extensive dataset, we provided evidence that cushion species are mainly found in families that occur in primarily cold, but also dry environments. This result should ideally be confirmed using micro-climatic data that better capture the climate actually experienced by plants (e.g. Anthelme et al., 2012), but it anyway supports previous results showing that the cushion life form was a key innovation that enabled the occupancy of extremely cold environments using phylogenetic comparative methods (Boucher et al., 2012) or physiological measurements (Larcher et al., 2010). Thus, the cushion life form likely represents an adaptive convergence of many angiosperms lineages to extremely cold and/or dry conditions, which phylogenetic and geographic extents are strikingly large. The cushion life form should thus be considered as one of the major key innovations that allowed Angiosperms to colonize arctic and alpine environments, among others (e.g. tussock grasses and perennial rosettes in temperate alpine environments, Körner, 1999; shrubs and caulescent rosettes in tropical alpine environments, Ramsay and Oxley, 1997). Moreover, the evolution of this life form may have played an important role in shaping alpine plant communities because cushion plants often facilitate less stress-tolerant species and lineages in severe environments, and play a keystone role for biodiversity maintenance in harsh alpine environments (Butterfield et al., 2013; Kikvidze et al., 2015).

Potential cradles and hubs of cushion diversity – Although cushion species are distributed in all arctic and alpine regions, there are large differences in the number of cushions among these regions. Indeed, 218 species of compact cushions can be found in South America and 207 species in temperate Asia. In contrast, 102 species are distributed in Europe, 80 in tropical Asia, 79 in Australasia, 43 in North America and only 18 in Africa. When correcting for the effect of cold and dry areas with a species-area relationship approach, we found that the regions of the world with the highest concentrations of cushion species were New Guinea, New Zealand, the Andes and Patagonia, the Himalayas and Hengduan mountains, the European Alps, and the Pyrenees (Table 2).

Among the main centers of cushion diversity, Tibet, Nepal, the Eastern Himalayas, and South-Central China have a high number of cushions but these belong to relatively few genera (Table 2), which indicates that these regions might have been places of extensive diversification for cushions. This is explained by the fact that among all current high elevation mountain ranges in the world the Himalayas are the ones that emerged from the oldest uplift (Yin and Harrison, 2000), which offered more time for cushion diversity to accumulate. The situation is rather similar in the European Alps and the Pyrenees, although fewer cushion species occupy these mountain ranges (Table 2) probably because they are younger and have a much smaller extent. All of these mountain ranges of Southern Eurasia have rather few endemic cushion species, suggesting that migration between them has largely contributed to their diversity.

In the Andes, migration between regions seems to have been an important contributor to the richness of cushions, as indicated by the fact that all Andean regions fell into the same floristic cluster (Fig. 4). The average number of species of cushions per genus is also lower than in Eurasia (Table 2), likely because altitudes above 2000 m are recent in the Andes (*i.e.* younger than 10 Ma, Hartley, 2003), leaving little time for cushion species to diversify. While Ecuador and Peru contain a rather high percentage of endemic cushions (Table 2), regions south of Peru possess few endemics, probably because alpine regions of the Southern Andes extend over large continuous areas while they are much more fragmented in the Northern Andes (Anthelme et al., 2014). Patagonia (*i.e.* Southern Chile and Southern Argentina) also has a relatively high number of different genera but few species of cushions per genus (Table 2). This could be due to its rather young history (Le Roux, 2012) but also probably reflects the fact that Patagonia has been a region connecting landmasses of the temperate Southern Hemisphere to South America (Crisp et al., 2009). This is supported by the fact that Patagonia forms a cluster with the Andes in our analysis (Fig. 4) and to a lesser extent with Antarctica (Fig. A1).

Finally, the case of New Zealand and New Guinea is singular because these regions bear traces of connections with other Austral regions but on the other hand possess many endemic cushion lineages. For example, the Southern island of New Zealand shares seven genera containing cushions with Patagonia: one of them is widespread (Oreobolus), others are largely distributed in the Southern Hemisphere (Astelia, *Abrotanella*, *Colobanthus*, *Gaimardia*), while *Donatia* and *Phyllachne* only occur in these two regions plus Tasmania. However, the high level of cushion endemism found in Southern New Zealand (63% of species) indicates that a large part of its cushion species may have originated through *in situ* diversification rather than from migration (for a discussion, see Winkworth et al., 2005). The situation is similar in New Guinea (72% of endemic cushion species but many genera shared with other regions of the Southern Hemisphere), although fewer species of cushions can be found there.

In contrast with regions highlighted above, arctic regions or the Rocky Mountains are not exceptionally cushion-rich. While the paucity of cushion species in arctic regions is probably a consequence of the young age of the Arctic combined with high extinction rates during glaciations of the Pleistocene (Brochmann and Brysting, 2008), the relatively low richness of the Rocky Mountains in terms of cushion species remains to be explained.

4.3. Future directions

While our list of cushion species is rather exhaustive, the phylogenetic and biogeographic scales used in this study have some limitations. First of all, the number of independent origins of the cushion life form that we estimated is very conservative, since we had no phylogenetic information within genera. Future studies using phylogenies resolved at the species level in families where the cushion life form is frequent (e.g. Caryophyllaceae, where 19 genera have cushion species) should provide more reliable estimates of the number of convergences towards this life form. Second, our demonstration that the cushion life form is adapted to cold and dry conditions is rather indirect since we used distribution data for whole families and not individual species. However, the fact that this adaptation has already been demonstrated in physiological experiments (Larcher et al., 2010) and with species-level phylogenetic analyses (Boucher et al., 2012) brings support to our conclusions.

An unaddressed question of this study is whether cushion generally spurred diversification, as has been shown in the genus *Androsace* (Roquet et al., 2013). In particular, it is of primary importance to determine whether cushions have increased speciation rates because they occupy highly fragmented habitats in mountains or if their extreme longevity (e.g. Morris and Doak, 1998; Halloy, 2002) leads to reduced extinction rates.

While our conclusions on the roles of different regions rely on taxonomic treatments and geographic subdivisions that are partly arbitrary, they however provide a first glimpse into the global biogeography of cushion species and artic-alpine plant biomes. Proper biogeographic reconstructions and diversification analyses with phylogenies resolved at the species level would be needed to accurately study the relative contributions of local diversification and migration to richness patterns in these different areas of the globe. In particular, such studies should provide interesting insights into whether or not the cushion life-form has repeatedly emerged as a response to cold and/or dry climates, and whether or not this life-form has spurred species diversification under extreme climates following mountain uplifts around the world.

5. Conclusion

Using a global, extensive catalogue of Angiosperms bearing the cushion life form, we have shown that the cushion life form is a convergent key innovation that has appeared at least 115 times independently in Angiosperms, providing the opportunity to colonize cold and dry environments. However, cushions are not randomly distributed in Angiosperms, suggesting that some traits might be prerequisite for this life form to appear. Cushions are present on all major mountain ranges in the World, but we have shown that the main centers of diversity are located in the Himalayas, the Andes, Patagonia and New Zealand. Importantly, while the Himalayas, the Northern Andes, and New Zealand might be cradles of cushion diversity, Patagonia might serve as hubs enabling floristic exchange between different regions. These results are of primary importance for understanding the origins of floras that have colonized cold and dry environments worldwide.

Acknowledgments

The authors are thankful to W. Thuiller for making available to us the data on the geographic distribution of angiosperm families and for interesting suggestions at earlier stages of this project. The authors also thank A. Cleef, R. Parson, and J. Wainwright-Klein for recent contributions to the cushion database. R. Salguero-Gomez and two anonymous reviewers provided insightful comments on the manuscript. This research was partly funded by the Station Alpine J. Fourier. SL received funding from the European Research Council under the European Community's Seven Framework Programme FP7/2007-2013 Grant Agreement no. 281422 (TEEMBIO). The authors are part of Labex OSUG@2020 (ANR10 LABX56).

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ppees.2016.03.002.

References

Akaike, H., 1973. Information theory and an extension of the maximum likelihood principle. Proc. Second Int. Symp. Inf. Theory, 267–281.

Anthelme, F., Buendia, B., Mazoyer, C., Dangles, O., 2012. Unexpected mechanisms sustain the stress gradient hypothesis in a tropical alpine environment. J. Veg. Sci. 23, 62–72, http://dx.doi.org/10.1111/j.1654-1103.2011.01333.x.

Anthelme, F., Jacobsen, D., Macek, P., Meneses, R.I., Moret, P., Beck, S., Jacobsen, D., Macek, P., Meneses, R.I., Moret, P., Beck, S., 2014. Biodiversity patterns and continental insularity in the tropical high andes. Arctic Antarct. Alp. Res. 46, 811–828.

Arakaki, M., Christin, P.-A., Nyffeler, R., Lendel, A., Eggli, U., Ogburn, R.M., Spriggs, E., Moore, M.J., Edwards, E.J., 2011. Contemporaneous and recent radiations of the world's major succulent plant lineages. Proc. Natl. Acad. Sci. U. S. A. 108, 8379–8384, http://dx.doi.org/10.1073/pnas.1100628108.

Arroyo, M.T.K., Cavieres, L.A., Peñaloza, A., 2003. Positive associations between the cushion plant *Azorella monantha* (Apiaceae) and alpine plant species in the Chilean Patagonian Andes. Plant Ecol. 169, 121–129.

Aubert, S., Boucher, F., Lavergne, S., Renaud, J., Choler, P., 2014. 1914–2014: a revised worldwide catalogue of cushion plants 100 years after Hauri and Schröter. Alp. Bot. 124, 59–70.

Badano, E.I., Jones, C., Cavieres, L., Wright, J., 2006. Assessing impacts of ecosystem engineers on community organization: a general approach illustrated by effects of a high-andean cushion plant. Oikos 115, 369–385.

Bell, C.D., Soltis, D.E., Soltis, P.S., 2010. The age and diversification of the Angiosperms revisited. Am. J. Bot. 97, 1296–1303.

Boucher, F.C., Thuiller, W., Roquet, C., Douzet, R., Aubert, S., Alvarez, N., Lavergne, S., 2012. Reconstructing the origins of high-alpine niches and cushion life form in the genus *Androsace* s.l. (primulaceae). Evol. (N. Y). 66, 1255–1268, http://dx.doi.org/10.5061/dryad.dp4rt4sh.

Box, E.O., 1981. Macroclimate and Plant Forms: an Introduction to Predictive Modeling in Phytogeography. Dr. W. Junk Publishers, The Hague/Boston/London.

Bray, J.R., Curtis, J.T., 1957. An ordination of upland forest communities of southern Wisconsin. Ecol. Monogr. 27, 325–349.

Brochmann, C., Brysting, A.K., 2008. The arctic –an evolutionary freezer? Plant Ecol. Divers. 1, 181–195.

Brummit, R.K., 2001. World geographic scheme for recording plant distributions.

Butterfield, B.J., Cavieres, L.A., Callaway, R.M., Cook, B.J., Kikvidze, Z., Lortie, C.J., Michalet, R., Pugnaire, F.I., Schöb, C., Xiao, S., Zaitchek, B., Anthelme, F., Björk, R.G., Dickinson, K., Gavilán, R., Kanka, R., Maalouf, J.P., Noroozi, J., Parajuli, R., Phoenix, G.K., Reid, A., Ridenour, W., Rixen, C., Wipf, S., Zhao, L., Brooker, R.W., 2013. Alpine cushion plants inhibit the loss of phylogenetic diversity in severe environments. Ecol. Lett. 16, 478–486, http://dx.doi.org/10.1111/ele.12070.

Cavieres, L.A., Brooker, R.W., Butterfield, B.J., Cook, B.J., Kikvidze, Z., Lortie, C.J., Michalet, R., Pugnaire, F.I., Schöb, C., Xiao, S., Anthelme, F., Björk, R.G., Dickinson, K.J.M., Cranston, B.H., Gavilán, R., Gutiérrez-Girón, A., Kanka, R., Maalouf, J.P., Mark, A.F., Noroozi, J., Parajuli, R., Phoenix, G.K., Reid, A.M., Ridenour, W.M., Rixen, C., Wipf, S., Zhao, L., Escudero, A., Zaitchik, B.F., Lingua, E., Aschehoug, E.T., Callaway, R.M., 2014. Facilitative plant interactions and climate simultaneously drive alpine plant diversity. Ecol. Lett. 17, 193–202, http://dx.doi.org/10.1111/ele.12217.

Christin, P.-A., Osborne, C.P., Chatelet, D.S., Columbus, J.T., Besnard, G., Hodkinson, T.R., Garrison, L.M., Vorontsova, M.S., Edwards, E.J., 2013. Anatomical enablers and the evolution of C4 photosynthesis in grasses. Proc. Natl. Acad. Sci. 110, 1381–1386, http://dx.doi.org/10.1073/pnas.1216777110.

Cockayne, L., 1912. Observations concerning evolution, derived from ecological studies in New Zealand. Trans. N. Z. Inst. 44, 1–17.

Crisp, M.D., Arroyo, M.T.K., Cook, L.G., Gandolfo, M.A., Jordan, G.J., McGlone, M.S., Weston, P.H., Westoby, M., Wilf, P., Linder, H.P., 2009. Phylogenetic biome conservatism on a global scale. Nature 458, 754–756, http://dx.doi.org/10.1038/nature07764.

Davies, T.J., Barraclough, T.G., Chase, M.W., Soltis, P.S., Soltis, D.E., Savolainen, V., 2004. Darwin' s abominable mystery: insights from a supertree of the angiosperms. Proc. Natl. Acad. Sci. U.S.A. 101, 1904–1909.

De Bello, F., Doležal, J., Dvorský, M., Chlumská, Z., Řeháková, K., Klimešová, J., Klimeš, L., 2011. Cushions of Thylacospermum caespitosum (Caryophyllaceae) do not facilitate other plants under extreme altitude and dry conditions in the north-west Himalayas. Ann. Bot. 108, 567–573, http://dx.doi.org/10.1093/aob/mcr183.

Edwards, E.J., Smith, S.A., C4 Grasses Consortium, 2010. Phylogenetic analyses reveal the shady history of C4 grasses. Proc. Natl. Acad. Sci. U. S. A. 107, 2532–2537, http://dx.doi.org/10.1073/pnas.0909672107.

Edwards, E.J., Osborne, C.P., Strömberg, C.A.E., Smith, S.A., 2010. The origins of C4 grasslands: integrating evolutionary and ecosystem science. Science 328, 587–591.

Fine, P.V., Ree, R.H., 2006. Evidence for a time-integrated species-area effect on the latitudinal gradient in tree diversity. Am. Nat. 168, 796–804.

Fitzjohn, R.G., Maddison, W.P., Otto, S.P., 2009. Estimating trait-dependent speciation and extinction rates from incompletely resolved phylogenies. Syst. Biol. 58, 595–611, http://dx.doi.org/10.1093/sysbio/syp067.

Gleason, H.A., 1922. On the relation between species and area. Ecology 3, 158–162.

Grabherr, G., Gottfried, M., Gruber, A., Pauli, H., 1995. Patterns and current changes in alpine plant diversity. In: Chapin, F.S., Körner, C. (Eds.), Arctic and Alpine Biodiversity: Patterns, Causes and Ecosystem Consequences. Springer, Berlin, pp. 167–181.

Halloy S.R.P., 2002. Variations in community structure and growth rates of high-andean plants with climatic fluctuations, in: Körner, C., Spehn, E.M. (Eds.), Moutain Biodiversity: A Global Assessment.

Hartley, A., 2003. Andean uplift and climate change. J. Geol. Soc. Lond. 160, 7–10.

Hauri, H., Schröter, C., 1914. Versuch einer Übersicht der siphonogamen polsterpflanzen. Bot. Jahrb Syst Pflanzengesch Pflanzengeogr 50, 618–656.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 25, 1965–1978, http://dx.doi.org/10.1002/joc.1276.

Ho, L.S.T., Ané, C., 2014. A linear-time algorithm for gaussian and non-Gaussian trait evolution models. Syst. Biol. 63, 397–408, http://dx.doi.org/10.1093/sysbio/syu005.

Ives, A.R., Garland, T., 2010. Phylogenetic logistic regression for binary dependent variables. Syst. Biol. 59, 9–26, http://dx.doi.org/10.1093/sysbio/syp074.

Körner, C., 1999. Alpine Plant Life. Springer, Berlin.

Johnson, X., Brcich, T., Dun, E.A., Goussot, M., Haurogné, K., Beveridge, K., Rameau, C.A., 2006. Branching genes are conserved across species. Genes controlling a novel signal in pea are coregulated by other long-distance signals. Plant Physiol. 142, 1014–1026, http://dx.doi.org/10.1104/pp.106.087676.

Kaufman, L., Rousseeuw, P.J., 1990. Finding Groups in Data: An Introduction to Cluster Analysis. John Wiley & Sons, Ltd., New York.

Kembel, S.W., Cowan, P.D., Helmus, M.R., Cornwell, W.K., Morlon, H., Ackerly, D.D., Blomberg, S.P., Webb, C.O., 2010. Picante: R tools for integrating phylogenies and ecology. Bioinformatics 26, 1463–1464.

Kikvidze, Z., Brooker, R.W., Butterfield, B.J., Callaway, R.M., Cavieres, L.A., Cook, B.J., Lortie, C.J., Michalet, R., Pugnaire, F.I., Xiao, S., Anthelme, F., Björk, R.G., Cranston, B.H., Gavilán, R.G., Kanka, R., Lingua, E., Maalouf, J.-P., Noroozi, J., Parajuli, R., Phoenix, G.K., Reid, A., Ridenour, W.M., Rixen, C., Schöb, C., 2015. The effects of foundation species on community assembly: a global study on alpine cushion plant communities. Ecology 96, 2064–2069, http://dx.doi.org/10.1890/14-2443.1.

Kleier, C., Rundel, P., 2009. Energy balance and temperature relations of *Azorella compacta*, a high-elevation cushion plant of the central Andes. Plant Biol. 11, 351–358, http://dx.doi.org/10.1111/j.1438-8677.2008.00115.x.

Larcher, W., Kainmüller, C., Wagner, J., 2010. Survival types of high mountain plants under extreme temperatures. Flora Morphol. Distrib. Funct. Ecol. Plants 205, 3–18, http://dx.doi.org/10.1016/j.flora.2008.12.005.

Le Roux, J.P., 2012. A review of tertiary climate changes in southern south america and the antarctic peninsula. Part 1: oceanic conditions. Sediment. Geol. 247–248, 1–20, http://dx.doi.org/10.1016/j.sedgeo.2011.12.001.

Lewis, P.O., 2001. A likelihood approach to estimating phylogeny from discrete morphological character. Data Syst. Biol. 50, 913–925.

Maddison, W.P., Maddison, D.R., 2015. Mesquite: a modular system for evolutionary analysis. Version 3.02 http://mesquiteproject.org.

Maechler, M., Rousseeuw, P., Struyf, A., Hubert, M., Hornik, K., 2015. Cluster: Cluster Analysis Basics and Extensions. R package version 2.0.1.

Mc Fadden, D., 1974. The measurement of urban travel demand. J. Public Econ. 3, 303–328.

Molenda, O., Reid, A., Lortie, C.J., 2012. The alpine cushion plant *Silene acaulis* as foundation species: a bug's-eye view to facilitation and microclimate. PLoS One 7, e37223, http://dx.doi.org/10.1371/journal.pone.0037223.

Molina-Montenegro, M.A., Badano, E.I., Cavieres, L.A., 2006. Cushion plants as microclimatic shelters for two ladybird beetles species in alpine zone of central Chile. Arctic Antarct. Alp. Res. 38, 224–227.

Morris, W.F., Doak, D.F., 1998. Life history of the long-lived gynodioecious cushion plant *Silene acaulis* (Caryophyllaceae), inferred from size-based population projection matrices. Am. J. Bot. 85, 784–793.

Mu, Q., Heinsch, F.A., Zhao, M., Running, S.W., 2007. Development of a global evapotranspiration algorithm based on MODIS and global meteorology data. Remote Sens. Environ. 111, 519–536.

Mu, Q., Zhao, M., Running, S.W., 2011. Improvements to a MODIS global terrestrial evapotranspiration algorithm. Remote Sens. Environ. 115, 1781–1800.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2013. vegan: Community Ecology Package. R package version 2. pp. 0–10.

Paradis, E., Claude, J., Strimmer, K., 2004. APE: analyses of phylogenetics and evolution in R language. Bioinformatics 20, 289–290.

Prentice, I.C., Cramer, W., Harrison, S.P., Leemans, R., Monserud, R.A., Solomon, A.M., 1992. A global biome model based on plant physiology and dominance, soil properties and climate. J. Biogeogr. 19, 117–134.

R Development Core Team, R., 2014. R: A Language and Environment for Statistical Computing. R Found. Stat. Comput., R Foundation for Statistical Computing. 10.1007/978-3-540-74686-7.

Ramsay, P.M., Oxley, E.R.B., 1997. The growth form composition of plant communities in the ecuadorian paramos. Plant Ecol. 131, 173–192, http://dx.doi.org/10.1023/A.;1;1009796224479.

Rauh, W., 1939. Über polsterförmigen Wuchs: Ein Beitrag zur Kenntnis der Wuchsformen der höheren Pflanzen. Nov. Acta Leopold 7, 272–505.

Raunkiaer, C., 1934. The Life Forms of Plants and Statistical Plant Geography. Oxford University Press, Oxford.

Richards, J., 2003. Primula. Timber Press, Portland.

Roquet, C., Boucher, F.C., Thuiller, W., 2013. Replicated radiations of the alpine genus *Androsace* (Primulaceae) driven by range expansion and convergent key innovations. J. Biogeogr. 40, 1874–1886, http://dx.doi.org/10.1111/jbi.12135.

Roy, J., Albert, C.H., Choler, P., Clément, J.-C., Ibanez, S., Lavergne, S., Saccone, P., Zinger, L., Geremia, R.A., 2013. Microbes on the cliff: alpine cushion plants structure bacterial and fungal communities. Front. Microbiol. 4.

Rudolph, E.D., 1965. Antarctic lichens and vascular plants: their significance. Bioscience 15, 285–287.

Schöb, C., Butterfield, B.J., Pugnaire, F.I., 2012. Foundation species influence trait-based community assembly. New Phytol. 196, 824–834.

Smith, S.A., Beaulieu, J.M., Donoghue, M.J., 2010. An uncorrelated relaxed-clock analysis suggests an earlier origin for flowering plants. Proc. Natl. Acad. Sci. U. S. A. 107, 5897–5902.

Spomer, G.G., 1964. Physiological ecology studies of Alpine cushion plants. Physiol. Plant. 17, 717, 724.

Stephenson, N.L., 1998. Actual evapotranspiration and deficit: biologically meaningful correlates of vegetation distribution across spatial scales. J. Biogeogr. 25, 855–870.

The Angiosperm Phylogeny Group, 2009. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: aPG III. Bot. J. Linn. Soc. 161, 105–121.

Umehara, M., Hanada, A., Yoshida, S., Akiyama, K., Arite, T., Takeda-Kamiya, N., Magome, H., Kamiya, Y., Shirasu, K., Yoneyama, K., Kyozuka, J., Yamaguchi, S., 2008. Inhibition of shoot branching by new terpenoid plant hormones. Nature 455, 195–200.

Vamosi, J.C., Vamosi, S.M., 2010. Key innovations within a geographical context in flowering plants: towards resolving Darwin's abominable mystery. Ecol. Lett. 13, 1270–1279, http://dx.doi.org/10.1111/j.1461-0248.2010.01521.x.

Webb, C.O., Ackerly, D.D., McPeek, M. a., Donoghue, M.J., 2002. Phylogenies and community ecology. Annu. Rev. Ecol. Syst. 33, 475–505, http://dx.doi.org/10.1146/annurev.ecolsys.33.010802.150448.

Weddel, H.A., 1857. Chloris Andina: Essai d'une Flore De La région Alpine Des Cordillères De l'Amérique Du Sud. Bertrand, Paris.

Werner, P., 1988. La Flore. Pillet, Martigny.

Wikstrom, N., Savolainen, V., Chase, M.W., 2001. Evolution of the angiosperms: calibrating the family tree. Proc. R. Soc. B Biol. Sci. 268, 2211–2220.

Yin, A., Harrison, T.M., 2000. Geologic evolution of the Himalayan-Tibetan orogeny. Annu. Rev. Earth Planet. Sci. 28, 211–280.

Zhao, Y., 2010. Auxin biosynthesis and its role in plant development. Annu. Rev. Plant Biol. 61, 49–64, http://dx.doi.org/10.1146/annurev-arplant-042809-112308.

Zachos, J., Pagani, M., Sloan, L., Thomas, E., Billups, K., 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. Science 292, 686–693, http://dx.doi.org/10.1126/science.1059412.

Zanne, A.E., Tank, D.C., Cornwell, W.K., Eastman, J.M., Smith, S.a., Fitzjohn, R.G., Mcglinn, D.J., Meara, B.C.O., Moles, A.T., Reich, P.B., Royer, D.L., Soltis, D.E., Soltis, P.S., Swenson, N.G., Warman, L., Hemmings, F., Leishman, M.R., Oleksyn, J., Beaulieu, J.M., 2014. Three keys to the radiation of angiosperms in freezing environments. Nature, http://dx.doi.org/10.1038/nature12872.