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

Florian C. Boucher[a,b,c,*], Sébastien Lavergne[a,b], Mireille Basile[a,b], Philippe Choler[a,b,d,e], Serge Aubert[a,b,d,e,1]

[a] Univ. Grenoble Alpes, LECA, F-38000 Grenoble, France
[b] CNRS, LECA, F-38000 Grenoble, France
[c] Institut für Systematische Botanik, Universität Zürich, Zollikerstrasse 107, CH-8008 Zürich, Switzerland
[d] Univ. Grenoble Alpes, SAJF, F-38000 Grenoble, France
[e] CNRS, SAJF, F-38000 Grenoble, France

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.

© 2016 Geobotanisches Institut ETH, Stiftung Ruebel. Published by Elsevier GmbH. All rights reserved.

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 helveti*ca, 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

* Corresponding author.
E-mail address: floflobouche r@gmail.com (F.C. Boucher).

[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
1433-8319/© 2016 Geobotanisches Institut ETH, Stiftung Ruebel. Published by Elsevier GmbH. All rights reserved.

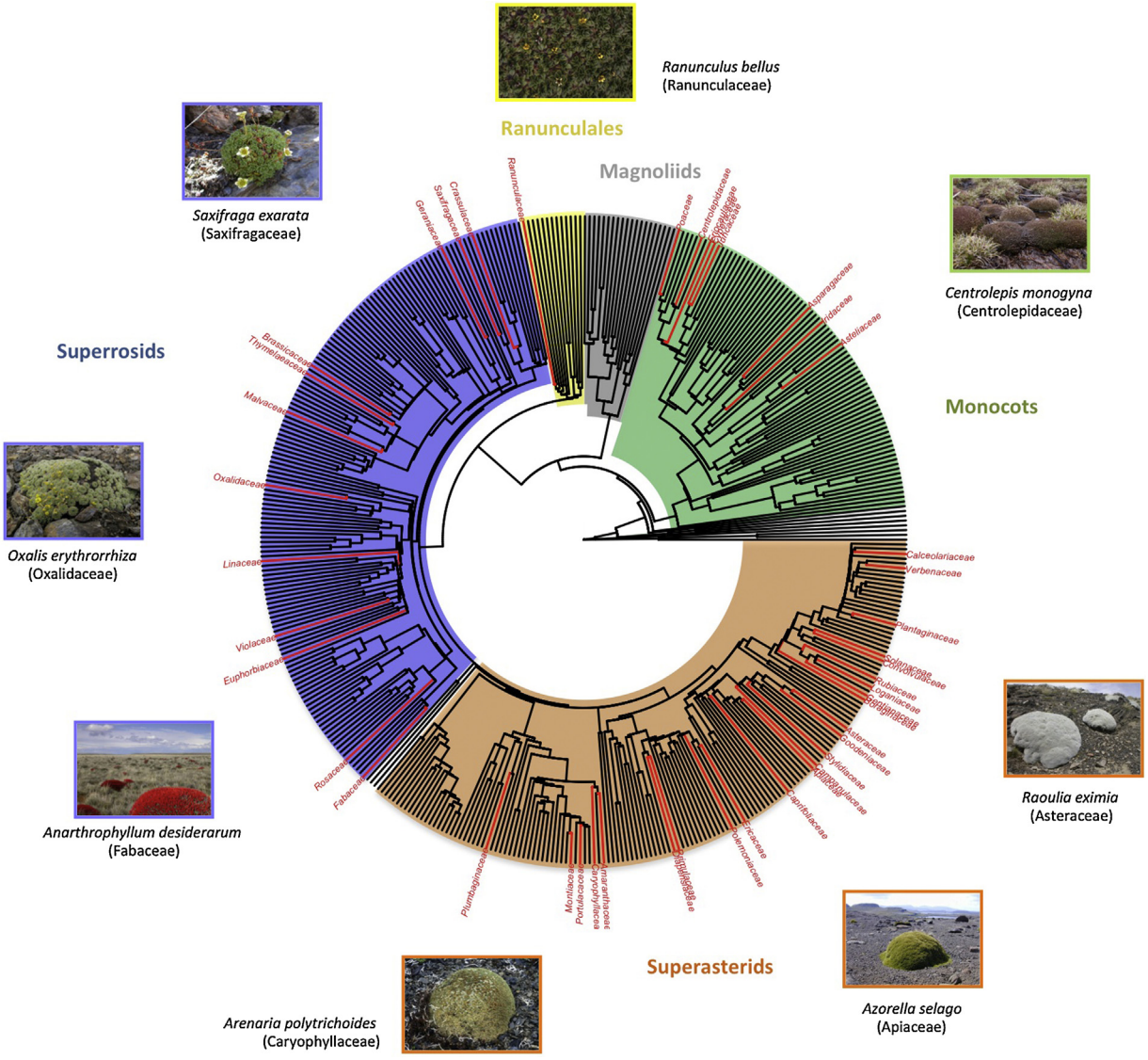

Fig. 1. Distribution of cushion species in Angiosperms. Each tip of this phylogenetic tree is an Angiosperm family (Zanne et al., 2014) and five major groups are underlined with different colors: Monocotyledoneae (green), Magnoliidae (grey), Ranunculales (yellow), Superrosideae (blue), and Superasterideae (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

Download English Version:

https://daneshyari.com/en/article/4400913

Download Persian Version:

https://daneshyari.com/article/4400913

Daneshyari.com