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Azorella compacta: survival champions in extreme, high-elevation environments

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Abstract. Cushion plants are life forms with a hemispherical or mat-like, prostrate canopy well adapted to the extreme conditions of cold regions that have appealed to scientists for their ability to cope with extreme environments in most mountains, arctic, and subantarctic regions of the world. They can buffer the effects of low temperature and drought and improve soil conditions, which makes them notable facilitator species. Living at the edge in the Atacama Desert is one such species, *Azorella compacta* (yareta or llareta), in the Apiaceae family that can reach much over 6 m (~20 ft) in diameter with a mat-like shape that tends to hemispherical growth form. *Azorella compacta* can be found in the dry Puna system, which spreads from northern Chile and Argentina to southern Peru and western Bolivia, between 3800 and 5200 m elevation, making it one of the woody plant species occurring at highest elevations in the world. In this deserted edge of the Atacama, nutrient limitation adds to other stressors such as water scarcity and high UV radiation. A compact canopy and the fact that they are embedded in resin prevent beneficiary species from growing within the cushion and condition how senesced leaves decompose inside the canopy. They can reach 3000 yr old and have to deal with episodic disturbance and herbivory events. Plants in such environments may potentially act as microbial refuges, and it could be expected that bacterial endophytes and mycorrhizal fungi have a main role in the functioning of these survival champions.

Key words: cushion plants; high-elevation ecosystems; long-lived plants; plant-microbe interactions; Puna.

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Cushion plants are life forms with a hemispherical or mat-like, prostrate canopy well adapted to the extreme conditions of cold regions that have appealed to scientists for their ability to cope with extreme environments in most mountains, arctic, and subantarctic regions of the world (Aubert et al. 2014). Their compact habit allows cushions to decouple microclimate inside the canopy from the surrounding environment. They can buffer the effects of low temperature and drought and improve soil conditions (Cavieres and Badano 2009). This feature makes them notable facilitator species that enhance survival of other plant functional groups living inside the cushion (Reid et al. 2010, Cavieres et al. 2014). The cushion habit is relatively widespread, as there have been identified 1309 cushion-forming species distributed in 272 genera and 63 families of angiosperms (Aubert et al. 2014).

Since the 1990s, their appeal has increased among ecologists and, as a consequence, knowledge about their growth form, functional variability, ecosystem role, and evolutionary origin (Reid et al. 2010, Boucher et al. 2016) has accrued remarkably. Some of the biggest among all cushion plants are found in the Andes, where species in the *Azorella* or *Bolax* genera can reach outstanding size (Badano and Cavieres 2006). Living at the edge in the Atacama Desert is one such monster plant, *Azorella compacta* (yareta or llareta), a species in the Apiaceae family that can reach much over 6 m (~20 ft) in diameter with a mat-like shape that tends to hemispherical growth form (Fig. 1). It catches the eye by its luxuriant light green amid the pale colors of desert. *Yareta* cushions are generally on a north-facing aspect and at an angle of about 20° from the horizontal to maximize catching solar radiation (Kleier et al. 2015). *Azorella compacta* can be found in the dry *Puna* system, which spreads from northern Chile and Argentina to southern Peru and western Bolivia, between 3800 and 5200 m elevation, making it one of the woody plant species occurring at highest elevations in the world (Kleier et al. 2015).

We came first across this species in 2016, working in Northern Chile to test the effects of cushion plants on soil microbial communities and their facilitation effect along environmental gradients. Work on cushion plants has been extensive in the Andes since the 1980s (e.g., Villagrán et al. 1978, Armesto et al. 1980, Alliende and Hoffmann 1983), and their facilitation effects have been widely documented (e.g., Cavieres and Badano 2009 and references therein), as well as their changes with elevation (Alliende and Hoffmann 1983, Badano and Cavieres 2006, Anthelme et al. 2017). But in the Lauca National Park and Atacama highlands (*Puna*), Chile, we found that *A. compacta* barely hosted any beneficiary species (Table 1), in sharp contrast to coexisting *Pycnophyllum* cushions (Anthelme et al. 2017) and *Azorella* species elsewhere (Badano and Cavieres 2006). As other cushion plants, *A. compacta* branches are tightly packed and make a thick canopy with a smooth, continuous surface that has important microclimate effects. Senesced leaves are kept in contact with the branch as it grows, producing a characteristic brown and white pattern if sectioned. In this deserted edge of the Atacama, nutrient limitation

Fig. 1. A large individual of *Azorella compacta* at 4600-m elevation in the Puna region at the edge of the Atacama Desert near the Chile-Bolivia border.

Table 1. Relative interaction index (RII; Armas et al. 2004, *Ecology* 85: 2682–2686) of *Azorella compacta* and *Pycnophyllum* sp in the Lauca and Sajama National Parks (Chile and Bolivia, respectively).

Species	Lauca National Park (Chile)† RII	Sajama National Park (Bolivia)‡ RII
Azorella compacta	−0.8	−1.00
Pycnophyllum sp	0.7	0.59

Notes: RII ranges −1 to +1, with positive values showing facilitation and negative values showing competition. In both cases, *A. compacta* appears as a strong competitor which does not allow other (beneficiary) species to grow into its canopy, in clear contrast to co-occurring cushion species like *Pycnophyllum* sp or other *Azorella* species.
† Unpublished.
‡ from Anthelme et al. (2017).

adds to other stressors such as water scarcity and high UV radiation. Plants in such environments may potentially act as microbial refuges (Roy et al. 2013), and in the dry Puna *A. compacta* cushions could play a main role as unique microorganisms shelters. The compact canopy and the fact that they are embedded in resin prevent beneficiary species from growing within the cushion and condition how senesced leaves decompose inside the canopy. Most likely the process is similar to peat formation, that is, an anaerobic process in which organic matter only decomposes in part, making this species a significant carbon sink.

Azorella compacta Phill. can reach 3000 yr old (Ralph 1978) although the typical age is around 850 yr; being such long-lived species means it has to deal with episodic stress and herbivory events. And so it does! Loads of resin protect *yaretas* against herbivores, and especially, some chemical compounds called terpenes that make up an important fraction of its dry mass and can be seen as droplets on the canopy and in the soil around the cushion. They are serious deterrent for herbivores, to the point that *A. compacta* is virtually free of them (Ralph 1978). Terpenes produced by *A. compacta* have high antimicrobial activity (Donoso et al. 2015) and contribute to protect the plant against pathogenic bacteria. Resin might also affect, thus, the structure and function of soil microbial communities around the cushion. This high chemical protection has

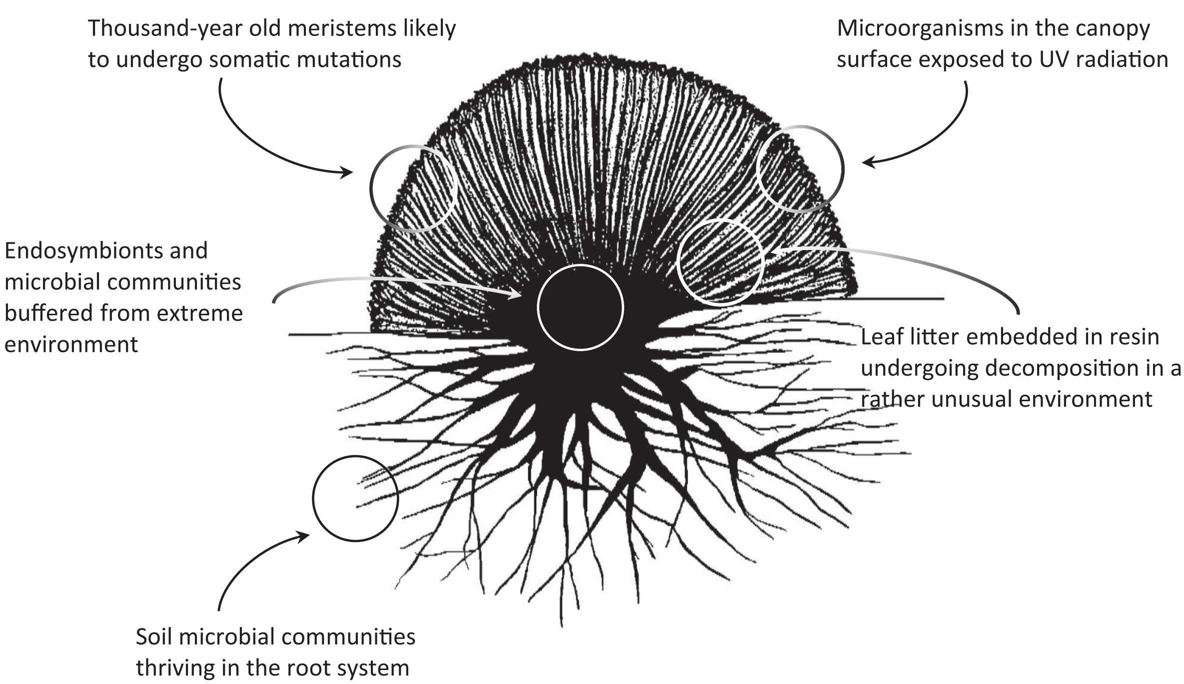

Fig. 2. Sketch of the structure of a cushion plant and points where research could provide important clues concerning the longevity and adaptation of these species to extreme environments.

drawbacks, however, as resin burns easily and thunderstorms lightning often set afire and kill the cushion. Nevertheless, and because of its compact structure, protected buds can restore back the canopy after burning in a process easily spotted in the field, as waves of green leaves cover charred canopy surfaces—witnesses of earlier fire events. In fact, most large *yaretas* show fire scars. The burning capacity and heating value made this species a favorite fuel among rural Aymara populations in the *Puna*. The nitrate mining industry, however, had strong negative impacts on *yareta* populations in the late 1800s and early 1900s, to the extent of being over-exploited in much of its geographical distribution range (Burton 2017). Because of the large amount of secondary compounds, mostly terpenes, *A. compacta* is frequently used in Andean popular medicine, showing a huge variety of positive health effects, including antimicrobial, anti-inflammatory, analgesic, antihyperglycemic, and many others (Wickens 1995).

Ralph (1978) made a nice recount of the main features of this outstanding Andean species, including a picture from the mid-20th century showing a really big *yareta*. She suggested that the biggest individuals would have been already harvested or remain only in remote areas. *Azorella compacta* extraction and transport were regulated in Chile in 1941, and it is strictly protected since 2008. Its recovery may last centuries although a relatively high number of small, 'young' *yareta* individuals can be easily found in some locations pointing to a comeback of the species (Kleier et al. 2015). Being in a severe environment with water shortage, low temperatures, and high irradiance plus the additional burden of producing defensive substances, reflects in a slow growth rate. Ralph (1978) reported an increase of 1.4 mm/yr, and Kleier et al. (2015) reported a radial growth of 0.4 cm/yr, although they acknowledged that determining its real growth rate is rather difficult.

An interesting question concerning long-lived plants like *A. compacta* is that they should face a wide range of abiotic and biotic threats over their lifespan. Thus, meristems of a 3000-year-old plant could have accumulated somatic mutations leading to within-organism genetic heterogeneity that may compromise its viability (Thomas 2012). Most deleterious somatic mutations are efficiently purged by intraorganismal selection (Pineda-Krch and Fagerström 1999) but there are beneficial mutations that are important sources of adaptive fitness (Pineda-Krch and Fagerström 1999). Intra-individual genetic variability may provide direct fitness benefits in the arms race with short-lived pests and pathogens through a phenotype patchwork. Through intraorganismal selection, long-lived plants can lose branches that are evolutionarily at selective disadvantage, preventing them from producing gametes (Groot and Laux 2016). In fact, the transmission of somatic mutations and the expansion of disease resistance gene families have been already evidenced in oak trees (Plomion et al. 2018). Potential conflicts and synergy effects between different genetic lineages within an individual provide an interesting subject for theoretical and empirical studies of multilevel selection (Pineda-Krch and Fagerström 1999).

Exploring these aspects in *A. compacta* and testing how long-lived species interact with their surrounding microbial communities may shed light on species co-evolution and adaptation to severe environments (Fig. 2). It could be expected that microorganisms, and particularly bacterial endophytes and mycorrhizal fungi, have a main role in the functioning of these survival champions.

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