

Cushion Plants from the Andes — an Overview of Current Knowledge and Some Research Needs

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ABSTRACT

Cushion plants are a unique plant life form adapted to the harshest conditions of the alpine and Antarctic environments around the world. Along the rugged topography of the Andes, cushion plants play a key role often serving as keystone species that create milder conditions and microclimates and provide shelter for other organisms. Additionally, some of them have the ability to grow under waterlogged soils in peatlands, where they have deep roots systems and low organic matter decomposition rates, resulting in high carbon accumulation rates. In this article, we will delve into the intriguing world of Andean cushion plants, exploring their adaptations and ecological roles. At the end, we raise and question some issues about cushion plants ecological processes and their implications for future studies.

RESUMEN

Las plantas en cojín son una forma de crecimiento única adaptada a resistir las duras condiciones de los ambientes alpinos y antárticos en todo el mundo. A lo largo de la abrupta topografía de los Andes, los cojines cumplen un papel fundamental al crear condiciones más moderadas y microclimas, además de proporcionar refugio a otros organismos. Además, algunas plantas en cojín tienen la capacidad de crecer en suelos saturados de agua como el de las turberas, donde tienen un sistema de raíces profundas y bajas tasas de descomposición de la materia orgánica, lo que resulta en altas tasas de acumulación de carbono. En este artículo, ahondaremos en el intrigante mundo de las plantas en cojín Andinas, explorando sus adaptaciones y roles ecológicos. Al final, planteamos algunas ideas y preguntas sobre los procesos ecológicos de las plantas cojín y sus implicaciones para futuros estudios.

INTRODUCTION

High-elevation ecosystems around the world are generally characterized by harsh environmental conditions, such as low extreme temperatures, high frequency of freeze-thaw events, high radiation, and poorly-developed soils that limit plant life. However, plants have developed fascinating adaptations to decouple from the atmospheric conditions and survive under stress (Körner 2003). One of these distinctive adaptations are cushion plants, which have modified their architecture to overcome the harsh conditions and maintain

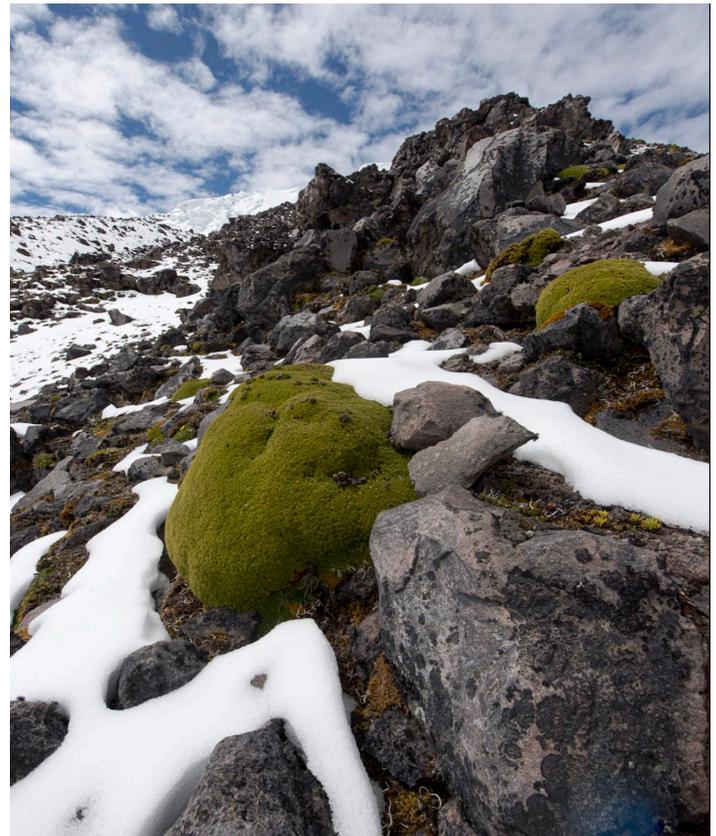


Figure 1. *Azorella aretioides* growing in a glacier foreland in Antisana Volcano, Ecuador. (Photo by Ricardo Jaramillo)

milder ones on their inside. They are particularly interesting to study because of their large plasticity when occupying different environments, being essential elements in high mountain peatland ecosystems. Here we present an overview of two most common cushion plants in the Andean region and some of the research needs to better understand their ecology and role in mountain peatland ecosystems.

Cushion plants are a unique plant life form that can be found in the Andes (South America), the Rockies (North America), the Tibetan Plateau, the Alps in Europe, Tasmania, New Zealand, and Tierra del Fuego (Arredondo-Núñez et al. 2009; Meng et al. 2013). They are characterized by a dense, compact, and rounded shape, resembling a cushion or pillow (Figure 1). Typically, their leaves are tightly packed near the top of the stems, and they have a deep root system. These features help them decouple from the environmental temperature by insulating on the inside and retaining warmer temperatures during the day, and slowly cooling down at night (Cavieres et al. 2006; Sklenář et al. 2016). Their dome-shape also allows them to store moisture, increase soil organic matter, and protect them from abrasive winds (Hager and Faggi 1990; Pyšek and Liška 1991; Cavieres et al. 2006).

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DIVERSITY AND DISTRIBUTION OF CUSHION PLANTS ALONG THE ANDES

Cushion plants comprise about 338 species within 34 plant families and are widely distributed in temperate Alpine and tropical mountain regions. Along the Andes, they can be found living under a wide humidity gradient from the humid northern Páramos of Colombia and Ecuador to the drier Puna of Perú and Bolivia. Some of the most widely distributed are *Plantago rigida* (observed from Colombia to Bolivia) and *Distichia muscoides* (observed from Colombia to Argentina), with others such as, *Paepalanthus karstenii* (observed in Venezuela and Colombia), *Azorella compacta*, *A. aretioides*, *A. pedunculata*, various species of the genera *Oreobolus*, and *Zameioscirpus* (observed from Ecuador to Bolivia), *Xenophyllum* spp. (observed from Colombia to northern Argentina and Chile), *Pycnophyllum* (observed from central Perú to northern Chile and southwest Bolivia), *Oxychloe andina* (observed from Perú to Argentina), *Astelia pumila* and *Donatia fascicularis* (observed in Chile), *Lysipomia muscoides* and *Patosia clandestine* (observed from Bolivia to Argentina and Chile), and *Aciachne pulvinata* (observed from Venezuela to Perú).

ROLE OF CUSHION PLANTS AS FOUNDATION SPECIES

In tropical mountain ecosystems such as Páramo and Puna, cushion plants play a crucial role in shaping the successional patterns along elevation gradients. They are considered to be ecosystem engineers and foundation species because they are the first ones to colonize newly formed ecosystems, such as deglaciated forelands, along with mosses, lichens, and some grasses (Cavieres et al. 2006; Sklenář 2009; Molenda et al. 2012; Reid and Lortie 2012; Schöb et al. 2012). Furthermore, because they can modify their inner microenvironment and create milder conditions, they can host other non-cushion plant species, serving as nurseries and allowing their establishment and growth in otherwise inhospitable conditions (Cavieres and Badano 2009; Anthelme et al. 2012).

The rugged topography of the northern Andes sets the perfect conditions for all these species to colonize a vast variety of steep terrains near glaciers, interspersed with concave glacial valleys with wetter conditions (Figure 2). Some, such as *Azorella*, *Xenophyllum*, and *Pycnophyllum* species, can colonize sandy and rocky slopes with poorly developed soils (Sklenar 2009), and lava flows and moraines (Suárez et al. 2015). Around 4100 m tussocks-grasses decline in abundance, and a dynamic transition takes place towards a cushion dominance. Here, the dominance of *Plantago rigida*, *Xenophyllum* and *Azorella* species, is particularly more pronounced in the more humid páramos of Colombia and Ecuador (Ramsay 1992, 1999; Sklenář 2000). As the soil gets wet and peatlands start to develop, only a few species have the ability to live under waterlogged conditions (Bosman et al. 1993). While commonly we associate the peatland vegetation around the world with

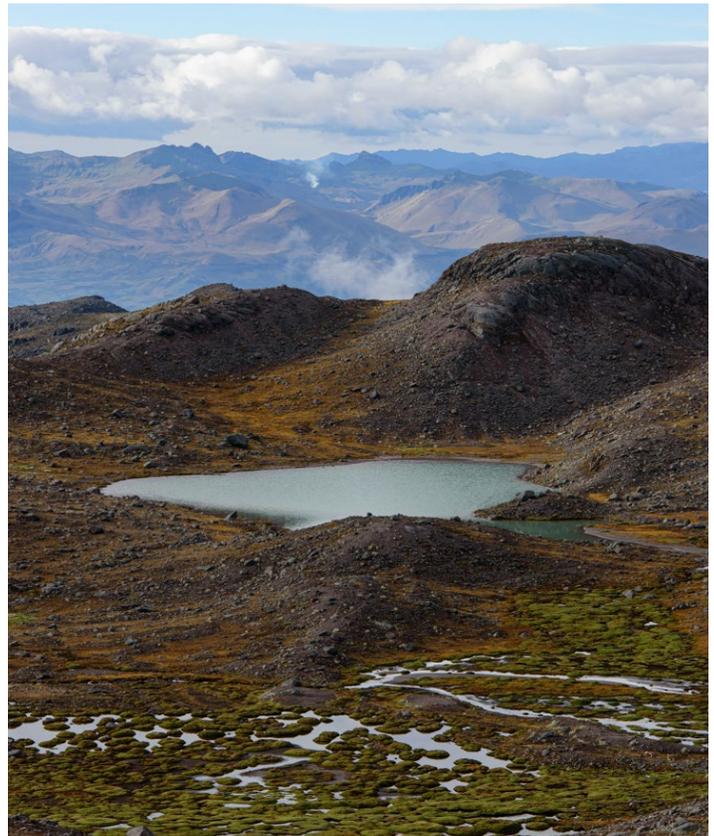


Figure 2. The rugged topography of the Andes allows the formation of peatlands in flat areas. (Photo by Ricardo Jaramillo)

soft bogs of *Sphagnum* mosses or grasses lawns of *Carex* and *Juncus* species, in the tropical Andes above 4100 m, peatlands tend to be dominated by cushion plants (Cleef 1981; Kleinbecker et al. 2010; Benavides et al. 2013; Suárez et al. 2021, 2023). Different regional terms describe the types of cushion peatlands found in the Andes, with “bofedales” being the most widespread.

At a landscape scale, when growing in a peatland, cushion plants are typically found on topographic depressions, being more abundant in the center where the water tables are close to the surface and more stable. As the water tables get deeper towards the edge, cushion plants become more dispersed, while herbs and grasses, still associated with wet conditions, become dominant and extend beyond the peatland (Coombes and Ramsay 2001). Zooming in at a site scale, cushion morphology creates a microtopography pattern of hollows and hummocks (Figure 3). In the lower points or hollows small water courses run through to temporary pools, where mosses and semi-aquatic species grow (Ruthsatz et al. 2020). At the same time, the top of the cushion or hummock is colonized by some opportunistic herbs and small shrubs, getting away from the water.

PRODUCTIVITY OF ANDEAN CUSHION PLANTS

One key characteristic of cushion-dominated peatlands in the Andean mountains is that they have some of the swiftest rates of net primary production and organic carbon generation, among all known peat-accumulating ecosystems



Figure 3. *Distichia muscoides* peatland microtopography of hummock and hollows, Colombia. (Photo by Violeta Martínez-Amigo)

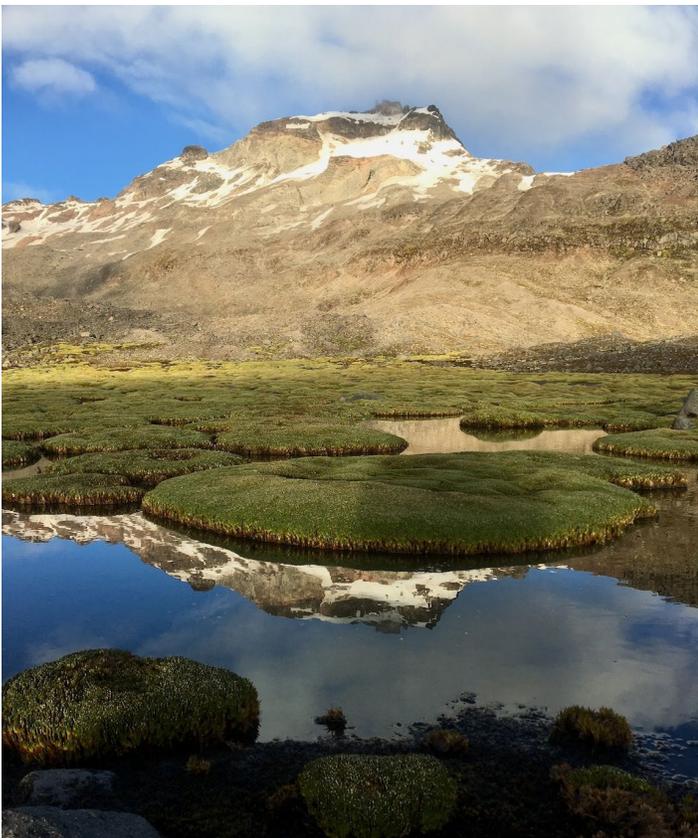


Figure 4. *Distichia muscoides* growing on a peatland near Mt. Carihuayrazo glacier, Ecuador. (Photo by Ricardo Jaramillo)

(Chimner and Karberg 2008; Cooper et al. 2010; Salvador et al. 2014). This high rate is due to particular factors that limit organic matter decomposition, such as a relatively frequent input of groundwater and rainfall, and wet anoxic soils (Cooper et al. 2015). Actually, some of the most rapid peat accumulation rates has been reported in the Chilean Andes (2 m per 1000 years), where *Oxychloe* cushion plant dominates (Earle et al. 2003).

In the Andean peatlands the two most common cushion plants are *Distichia muscoides* and *Plantago rigida* (hereafter referred to as their genus name) (Bosman et al. 1993; Coombes and Ramsay 2001; Benavides et al. 2013). According to Cleef (1978), both species constitute cushion peatlands at high elevations (3000–5200 m) in the Puna and Páramo, covering a large latitudinal gradient. This elevation gradient in the northern Andes of Colombia starts in the graminoid and bamboo Páramos, where we can find cushions in boggy valleys and former lakes between 3600–4200 m (Niemann and Behling 2008). In Ecuador the pattern is slightly different, with a peak dominance of both species above 4200 m, with dispersed abundance of *Plantago* at lower elevations and *Distichia* being highly dominant at the top range of the elevation distribution range (Figure 4) (Suárez et al. 2023).

When present in peatlands *Plantago* and *Distichia* are known to accumulate carbon underground in their roots and senescent leaves. By keeping senescent leaves on short stems, they can retain more humidity, and slow down decomposition of organic matter, making them highly efficient to incorporate organic carbon into the soil. Despite this, their root systems can be very different; on one side *Distichia* has deeper roots (>50 cm) that grow indefinitely from the terminal end of the stem, while the lower parts gradually die off, resulting in a high productivity of 2000-2800 g m⁻² yr⁻¹. On the other side, *Plantago* has 1.4 more root biomass than *Distichia*, but shorter roots and a lower annual root production (~1000 g m⁻² yr⁻¹) (Ruthsatz 2012; Palabral Aguilera 2013; Suárez et al. 2021). The resistant vegetal structure that characterizes both species prevents its decomposition, thus remaining in peat soil for long periods (Chimner and Karberg 2008; Cooper et al. 2010, 2015; Benavides et al. 2013).

While some studies have looked into the aboveground biomass (AGB) and productivity patterns of both species, more research is still needed to understand these patterns along nutrient, water and elevation gradients. Regarding *Plantago* the AGB of small to large cushions can range between 1700-5500 g m⁻² (Jaramillo et al. 2023) with a potential contribution of 28% of the total AGB of *Plantago*-dominated peatlands (Suárez et al. 2023). Moreover, *Plantago rigida* can store nearly 16 times more carbon (Mean ± SE: 13.3 ± 1.2) (Jaramillo et al. 2023) than other species of the same genus, such as *Plantago tubulosa* (0.81 Mg C ha⁻¹) (Yanqui et al. 2012), raising the importance of this species in the carbon accumulation of peatlands.

When comparing both species' carbon accumulation patterns, *Plantago* has higher net productivity than *Distichia*. The mean net ecosystem exchange reported in *Plantago* peatlands of Ecuador -0.69 g CO₂ m⁻² hr⁻¹ (Sánchez et al. 2017) were greater than those reported for *Distichia* in Colombia (-0.04g CO₂ m⁻² hr⁻¹) (Martínez-Amigo and Benavides 2023). Also, *Distichia* productivity using cranked-wire method ranged between 2.1 to 10.9 g C m⁻² day⁻¹ (Cooper et al. 2015; Planas-Clarke et al. 2020). Additionally, in terms of carbon storage, *Plantago* has the higher values (7 to 24 kg C m⁻²) (Jaramillo et al. 2023) when compared to *Distichia* (3.7-19.5 kg C m⁻²) (Martínez-Amigo and Benavides 2023). These variations may be attributed to differences in ecological niches, environmental factors, or management practices. Since they play an important role in primary production and soil carbon accumulation, their ecology is crucial for high Andean peatlands functioning. Thus, we underscore the importance of generating more data for a better understanding of the carbon dynamics of these ecosystems.

Within the vast scope of Andean cushion peatlands, there exists a rich variety of knowledge in different fields, and many of them still present gaps and uncertainties, wait-

ing to be explored. These gaps in our understanding serve as keystones towards new research horizons that spark our curiosity. Below, we raise and question some issues about ecological processes and their implications for future studies.

TOPICS FOR FUTURE RESEARCH

Phytoremediation. Andean cushion plants can grow whether on peatlands, or wet meadows with mineral soils (especially in the Puna) (Chimner et al. 2019). Along the Andean region we commonly associate *Distichia* cushions with deep-peaty soils, however they can also colonize sandy and coarse soils, associated with areas recently available after glacier retreat and mineral deposits of rivers (Figure 5). Furthermore, *Plantago* habitat is also related to soils with high mineral content, especially silver and iron concentrations, which at high concentrations could be toxic for other species (Bosman et al. 1993). Moreover, the use of plants from Juncaceae and Plantaginaceae families has been reported for bioremediation of heavy metal contamination (Otoya Fernández 2023). Plant species such as *Distichia muscoides* are classified as hyperaccumulators because of their capacity to remove heavy metals from water sources (Zimmer et al. 2018), opening a set of new research questions about the range of soil conditions where cushion plants can establish and grow.

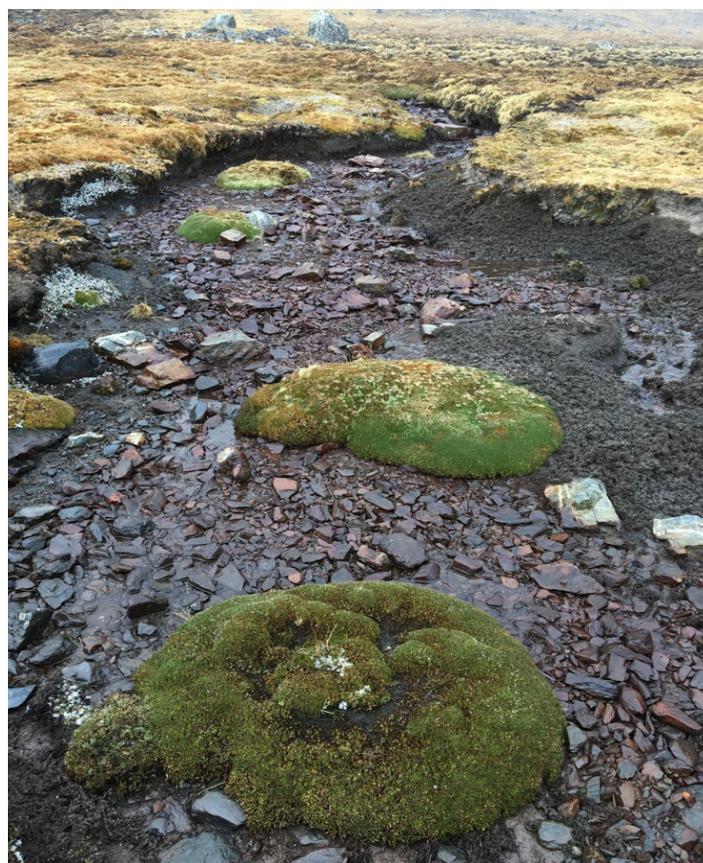


Figure 5. *Distichia muscoides* growing on a sandy and coarse soil in the Cordillera Real, Bolivia. (Photo by Violeta Martínez-Amigo)



Figure 6. Cushion collapse in El Cocuy National Park, Colombia. (Photo by Violeta Martínez-Amigo)

Cushion collapse. The ongoing climate change has affected peatland hydrology in recent years due to changes in the precipitation regimes or extreme and long droughts (Oyague and Cooper 2020). Recent observations in a Colombian cushion peatland indicated grasses proliferating in the cushion's surface and sinking of the central area, resulting in cushion collapse (Figure 6). Different hypotheses have been raised to explain the collapse; however, the water table drawdown and soil warming could be a plausible answer. Drier and warmer conditions in a peatland will lead to increased soil oxidation and decomposition rates. When water tables are high, the soil remains anaerobic, and the organic matter accumulates faster than it decomposes. But, under aerobic conditions, microbial activity accelerates carbon decomposition, enhancing the mineralization of the soil and causing peat subsidence, possibly resulting in cushion sinking. Despite this recent phenomenon drawing the attention of the scientific community, Bosman et al. (1994) argues that the collapse and replacing of *Plantago* cushions by *Oreobolus cleefi* is related to a development phase of peatlands, and cushion collapse could be a consequence of autogenic factors. In this sense, more research is needed to understand the successional patterns and the effects of extreme environmental conditions to cushion plant physiology and interspecific relations.

Climate change effects. Under the climate change context, with increasing mean temperatures, changes in

precipitation patterns, and glacier melts, the range and distribution of *Distichia* and *Plantago* could be affected. These species are usually found in environments shaped by glacier retreat and influenced by meltwater sources, however, their connection to glacier water is still debated. A particular case is the *Distichia*-dominated peatland of “El Valle de los Cojines” (El Cocuy, Colombia), where cushions are collapsing because of a decreased input of glacier water in recent years. The glacier-fed stream that runs through the center of the peatland carries less and less water than before. Some studies suggest that in the drier Puna the hydrology of cushion peatlands depends directly on glaciers, which ensure a constant water supply for maintaining stable water tables (Verzijl and Quispe 2013; Loza Herrera et al. 2015). However, recent studies propose that they do not necessarily depend on that hydrologic resource and unexpected factors are affecting cushion mortality (Oyague and Cooper 2020).

The relationship between low water table and the proliferation of species adapted to drier conditions was reported by Martínez-Amigo and Benavides (2023), showing different trajectories of plant composition, with decreasing cushion cover and increased abundance of grasses. These changes in species composition raise questions about the successional patterns of host cushion species and the interspecific relations with other plant life forms. In a context of less precipitation and decreasing water table levels species

with a high dependence on water supply, such as *Distichia*, could reduce its ecological niche, while others such as *Plantago* would expand it. There are complex interactions between environmental factors that shape different biotic relations that need to be addressed to understand the successional patterns in these ecosystems.

Cushion plants are peat-forming species and changes in the species composition from cushion plant dominance towards other types of vegetation could result in alterations in the peat accumulation patterns. Thus, concerns arise about how climate change will affect cushion-dominated peatland carbon accumulation patterns and methane emissions. Moreover, there are few studies describing the dynamics of carbon accumulation and greenhouse gas fluxes (CO₂ and CH₄) in Andean cushion peatlands as discussed previously with large differences between *Plantago* and *Distichia*. Despite these differences being attributed to site specific characteristics (e.g., grazing, herbivory, and drainage) we still need to understand how environmental factors are driving the carbon cycle in cushion peatlands.

CONCLUSION

The theoretical framework of the Andean cushion plants presents countless possibilities for novel research. We have identified some of the questions and knowledge gaps in the ecology of these unique plant life forms that we need to address to expand our comprehension of Andean peatlands. The challenges we underscore are: 1) the applications of cushion plants in bioremediation to remove heavy metals from water sources, 2) the changing drivers that could cause cushion collapse, 3) the glacier melting effect on peatland hydrology, 4) the successional patterns on cushion species and their interspecific relations, 5) the carbon accumulation patterns, and 6) methane emissions of cushion peatlands.

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