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ORIGINAL ARTICLE

Moss-driven facilitation promotes species coexistence in Andean páramo peatlands

Liz Ávila-Rodríguez[1,2] · Clara Tinoco-Ojanguren[4] · Miguel Martínez-Ramos[5] · Tania Sánchez-Ortiz[6] · Alfonso Valiente-Banuet[2,3]

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Abstract

Andean páramo peatlands are fragile high-altitude ecosystems characterized by frequent fog, intense seasonal solar radiation, strong daily temperature fluctuations, water saturation, and nutrient scarcity. These extreme conditions make them ideal systems for examining facilitative plant interactions and their influence on microclimate, soil nutrient dynamics, and biodiversity. We recorded 65 plant species and 5,368 individuals; 54% of the species and 89% of the individuals occurred on moss-dominated hummocks that covered only 29% of the surface. These structures, supported by the bamboo *Chusquea tessellata*, host extensive mats of *Sphagnum magellanicum*, *Kurzia capillaris*, *Breutelia squarrosa*, and *S. cuspidatum*. Strong species co-occurrence within these microhabitats suggests that there are positive interactions among mosses, liverworts, and vascular plants. At the hummock scale, we identified 5,299 species associations and nine non-vascular species acting as potential facilitators. Generalized linear models showed that non-vascular richness significantly predicted vascular diversity, particularly in combination with hummock area. By forming the basal substrate, mosses and liverworts regulate key ecological processes, such as water capture, infiltration, and nutrient cycling. Vertically structured assemblages played complementary roles: basal and middle layers dominated by *K. capillaris*, *S. cuspidatum*, and *B. squarrosa* enriched soils with nitrogen, phosphorus, and carbon; *S. magellanicum*, typically found in intermediate layers, buffered temperature; and upper *Frullania convoluta* cushions increased relative humidity during dry periods, while basal strata retained moisture. These findings demonstrate that moss-mediated interactions shape species-rich microsites, providing insights into biodiversity conservation and the restoration of Andean peatlands.

Keywords Andean páramo · Ecological facilitation · Mosses · Peatlands · Plant–plant interactions · Soil–water dynamics

✉ Alfonso Valiente-Banuet
avali@unam.mx; avalib@gmail.com

[1] Posgrado en Ciencias Biológicas, Universidad Nacional Autónoma de México, Edificio D, 1° Piso, Circuito de Posgrados, Ciudad Universitaria, Coyoacán, Ciudad de México 04510, México

[2] Departamento de Ecología de la Biodiversidad, Instituto de Ecología and Centro de Ciencias de la Complejidad, Universidad Nacional Autónoma de México, A.P. 70-275, 04510 Ciudad de México, México

[3] Centro de Ciencias de la Complejidad, Universidad Nacional Autónoma de México, 04510 Ciudad de México, México

[4] Departamento de Ecología de la Biodiversidad, Instituto de Ecología, Unidad Hermosillo, Universidad Nacional Autónoma de México, Luis Donaldo Colosio Esq, Sahuaripa, Sonora 83000 Hermosillo, México

[5] Instituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional Autónoma de México, Campus Morelia, Antigua Carretera a Pátzcuaro #8701, Col. Ex- Hacienda de San José de la Huerta, Michoacán 58190 Morelia, México

[6] Centro Internacional de Investigación de Economía Social y Solidaria, Universidad Iberoamericana, Campus México City, Prolongación Paseo de Reforma 880, Lomas de Santa Fe, 01219 Ciudad de México, México

Introduction

Páramos are high-elevation tropical ecosystems of the northern Andes, occurring between 3,000 and 5,000 masl in landscapes that lie between the upper forest boundary and the lower glacial zone (Jiménez-Rivillas et al. 2018; Peyre et al. 2021). Despite their high altitude and extreme temperature fluctuations, paramos are biodiversity hotspots with high species richness and endemism (Londoño et al. 2014; Peyre et al. 2018). Abiotic filters such as soil chemistry, water dynamics, and nutrient availability alone cannot fully explain the diversity patterns observed in these systems (Weiher and Keddy 1995). Ecological interactions, particularly competition (Weiher and Keddy 1995; Hájek and Adamec 2009) and facilitation (Bertness and Callaway 1994; Brooker et al. 2008; Stachowicz 2001), also play an important role in determining how species coexist and how communities are structured (Bu et al. 2013; Callaway and Walker 1997). Bertness and Callaway (1994) provided one of the first comprehensive syntheses showing that facilitative interactions can be major drivers of community assembly under stressful environmental conditions. Stachowicz (2001) described facilitation as an ecological process in which at least one species benefits without harming the other, while Brooker et al. (2008) emphasised its contribution to maintaining ecosystem function and stability. In this study, we test the idea that positive interactions are key to community structure and diversity in páramo peatlands.

Facilitation has been documented across a wide range of ecosystems, from arid lowlands to alpine tundra, glacier forelands, and wetlands (Callaway 2007). In these environments, facilitation operates through several mechanisms that modify the surrounding physical conditions and improve the chances of establishment for other species (Bruno et al. 2003; Hunter and Aarssen 1988). Processes such as water retention, temperature buffering, nutrient accumulation, and protection from radiation help reduce abiotic stress (Callaway 2007) and expand the realized niche of neighbouring plants, counteracting the constraints imposed by competition (Bruno et al. 2003). Over the past two decades, growing empirical evidence has shown that facilitation is fundamental for maintaining species diversity in stressful environments (Anthelme et al. 2012; Bertness and Callaway 1994; Hacker and Gaines 1997; Michalet et al. 2014). According to Hacker and Gaines (1997), positive interactions promote biodiversity by increasing survival and recovery under harsh conditions and by linking species into interaction networks along stress gradients, where facilitation tends to dominate under moderate to severe stress. Therefore, facilitation should be considered as a central ecological process influencing community structure and ecosystem stability in extreme environments (Brooker et al. 2008).

Growing evidence from periglacial zones of Patagonia (Gavini et al. 2020), the Central Andes (Zimmer et al. 2018), and the páramo (Smith 1984; Llambí et al. 2021; Pérez 1997) indicates that non-vascular organisms—particularly mosses (Gavini et al. 2020; Llambí et al. 2021), lichens (Llambí et al. 2021), and mixed biological soil crusts (Pérez 1997; Zimmer et al. 2018)—play a crucial role in stabilizing the substrate, retaining moisture, and protecting seedlings from frost and wind, thereby facilitating early vascular plant establishment. As succession proceeds, plant–plant interactions become increasingly important in structuring alpine communities, influencing species establishment, survival, and spatial organization (Anthelme et al. 2014; Cavieres et al. 2014). Nevertheless, the contribution of non-vascular plants to community assembly in páramo peatlands remains poorly understood. In contrast, facilitative interactions among vascular plants are well documented in páramo ecosystems. Shrubs such as *Hypericum* spp. (Ayarza-Páez et al. 2022; Cáceres et al. 2015; Farji-Brener et al. 2009; Ramírez et al. 2015) and *Baccharis prunifolia* (Bueno and Llambí 2015) mitigate abiotic stress by buffering temperature extremes, reducing solar radiation, and increasing ambient humidity—conditions linked to greater plant diversity. Symbiotic associations, particularly mycorrhizal partnerships common among páramo species, further enhance stress tolerance by improving nutrient uptake and sustaining plant performance under limiting conditions (Diaz et al., 2024). Likewise, cushion-forming nurse plants improve microsite conditions by accumulating organic matter and nutrients, thereby promoting seedling establishment (Llambí et al. 2018).

Mosses, particularly *Sphagnum* spp, dominate peatlands. There, flooded, anoxic, and acidic conditions foster organic matter accumulation but constrain nutrient availability, creating oligotrophic environments that restrict vascular plant establishment (Gornall et al. 2011; Heijmans et al. 2002; Rydin and Jeglum 2013). Most peatlands exhibit a distinct microtopography characterized by hummocks, valleys, and hollows that differ in aeration, moisture, and nutrient status (Rydin and Jeglum 2013). Hummocks, mainly formed by peat mosses, provide elevated, drier, and more aerated microsites that significantly influence species composition and ecosystem processes. Studies in boreal (Uppsala, Sweden; Rydin 1993) and temperate mires (Orivesi, Finland; Gong et al. 2020) show that *Sphagnum* species coexist along these vertical gradients by occupying niches defined by moisture-related physiological traits such as water retention and desiccation tolerance. For example, *S. fuscum* dominates drier hummocks, whereas *S. balticum* and related species prevail in wetter hollows but decline under desiccation stress (Rydin 1993). These habitat preferences reduce

direct competition and promote coexistence through trait-based niche differentiation (Gong et al. 2020; Rydin 1993).

Beyond spatial partitioning, *Sphagnum* species modify their physical and chemical environment, creating microhabitats that support other non-vascular plants (e.g., *Kurzia pauciflora*; Albinsson 1997), vascular species (Heijmans et al. 2001), and microbial communities such as algae and cyanobacteria that influence nutrient dynamics (Hooper 1981). Mosses promote the establishment and growth of vascular plants mainly by altering the physical and chemical environment. In boreal and temperate peatlands, these effects have been attributed to microclimate regulation, soil moisture retention, protection from environmental stress, and nutrient accumulation (Carlsson and Callaghan 1991; Gornall et al. 2011). The overall effect depends on moss depth: shallow layers can enhance vascular plant growth by maintaining warmer soils and improving nutrient access, whereas deeper mats may reduce nutrient availability and soil warming, thereby limiting positive interactions (Gornall et al. 2011). Comparable mechanisms are likely in tropical alpine systems, where *Sphagnum*-dominated páramo peatlands form hummocks that influence nutrient distribution and generate localized enrichment zones (Bosnian et al. 1993). In addition, belowground associations such as mycorrhizae may further modulate nutrient cycling and plant coexistence (Silva et al., 2023).

However, despite this potential, the role of mosses in shaping vascular plant diversity through such mechanisms remains unexplored in the páramo. These systems offer a great opportunity to investigate how facilitative interactions shape plant communities in extreme environmental conditions. Facilitation among plant species has traditionally been assessed through experimental approaches or trait-based frameworks (Callaway 2007). However, observational data have also been used to infer facilitative interactions based on non-random co-occurrence patterns (Valiente-Banuet and Verdú 2007, 2008). In this study, we evaluated whether non-vascular plants contribute to the richness of vascular plants using both co-occurrence and model-based analyses. We propose that facilitation acts as a major driver in páramo peatland biodiversity, with mosses disproportionately contributing to diversity through environmental modification. Our hypotheses were: (1) vegetation patterns in peatlands are non-random and concentrated in species-rich hummocks; (2) hummocks create vertically stratified microhabitats that promote coexistence along gradients of moisture and nutrient availability, from waterlogged, nutrient-rich bases to drier, nutrient-poor tops; and (3) mosses influence vascular diversity by altering abiotic conditions—temperature, humidity, nutrient levels (C, N, P), and water retention—thereby enhancing the capacity of hummocks to support diverse plant assemblages. Hypotheses 1 and 2 were tested through spatial association and within-hummock diversity analyses, while hypothesis 3 was addressed through measurements of moss dominance, hummock structure (height, area, layering), microclimate, and soil nutrients. Finally, we also considered dispersal filtering as an alternative explanation for vegetation aggregation, analysing the dispersal traits of vascular plants to assess the potential role of wind- and water-mediated seed transport (Cavieres and Arroyo 2001; Soons et al. 2017).

Materials and methods

Study site

Chingaza National Natural Park (PNN Chingaza) is situated on the eastern flank of the Cordillera Oriental in the Colombian Andes (Fig. 1). Its glacially shaped landscape includes U-shaped valleys, cirques, moraines, and numerous lagoons (Vargas and Pedraza 2004). The study site (4.51696° N, −73.70607° W) is a high-Andean peatland dominated by Sphagnum species, forming swampy vegetation that gradually transitions into drier páramo areas. As in other páramos, environmental conditions are harsh, with acidic and shallow soils, permanent water saturation, pronounced daily temperature fluctuations, intense ultraviolet radiation, high humidity, and strong winds (Vargas and Pedraza 2004).

The study site, located at 3415 masl, displays the typical microtopography of a high-Andean peatland, with well-defined hummocks, hollows, and mats (Cleef 1981; Schmidt-Mumm, et al., 2012). The climate is humid, with annual precipitation between 2800 and 3000 mm and a unimodal rainfall pattern marked by a short dry season from December to March (Vargas and Pedraza 2004). Frequent fog and dew, particularly during dry periods, help sustain high moisture levels throughout the year (Berrones et al. 2024).

The vegetation is dominated by *Chusquea tessellata*, a bamboo species well adapted to waterlogged conditions. Its dense branching provides a structural framework that supports the establishment of bryophytes, leading to the formation of elevated mounds above the water table. These hummocks exhibit marked vertical stratification: *Sphagnum* mosses dominate the wetter basal layers, whereas other bryophytes such as *Pleurozium schreberi*, *Campylopus* spp., and *Breutelia* spp. are more frequent along the drier upper margins (Sánchez-M. et al., 1989).

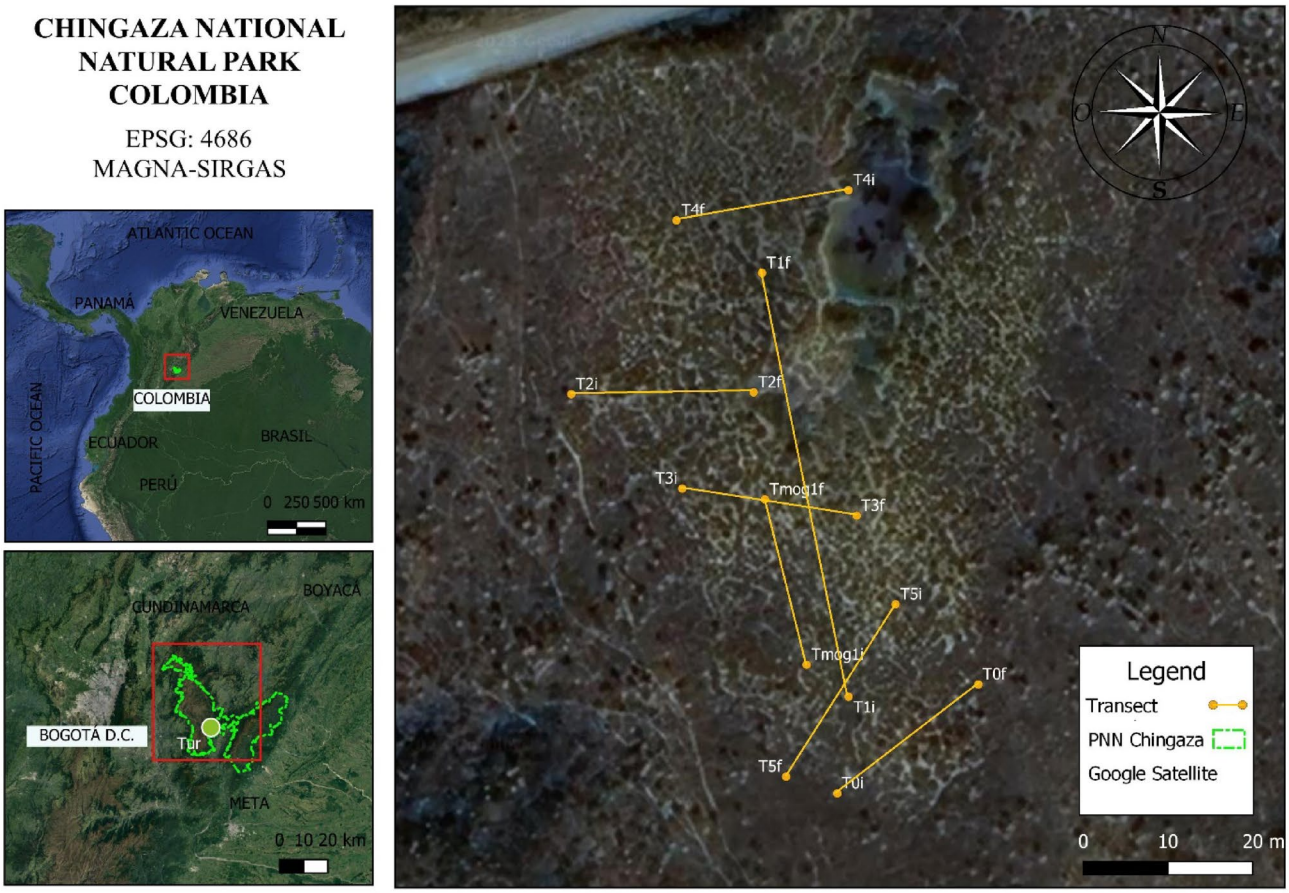


Fig. 1 Location of Chingaza National Natural Park (PNN Chingaza) in the Eastern Cordillera of Colombia (a, b). Distribution of sampling transects within the study peatland (c). Transects T1–T4 were used for analyses at the peatland scale, whereas T5M and T6M correspond to the hummock-scale survey

Assessing Spatial association patterns

Peatland-scale species associations

To characterize species associations at the peatland scale, we used a point-intercept line sampling method along one 50 × 10 m transect and four 20 × 2 m transects (T1–T4), covering a total area of 820 m² (Fig. 1). The first, larger transect was established during a pilot phase to assess vegetation heterogeneity. Based on these results, subsequent transects were standardized to 20 × 2 m to improve sampling representativeness and to avoid transitions between hummocks, marginal upland zones, and flooded areas within the peatland.

Along each transect, vegetation was recorded using the point-intercept method. Each sampling point corresponded to a plant intercepted by the measuring tape, with variable distances between points depending on vegetation density. At each intercept, we identified the plant and noted its position relative to microtopographic features (hummock or inter-hummock valley). This approach captured structural and compositional variation without relying on fixed-size quadrats. Additionally, we recorded all plant species (vascular and non-vascular) associated with the hummock or valley at each position. For vascular plants, each intercepted individual was recorded separately; clonal shoots were treated as independent individuals when separated by at least 2 cm of bare substrate or moss. For non-vascular plants (mosses, liverworts, lichens), the species covering the intercept was recorded. This method provided both species identity and microsite context (hummock vs. valley) for every sampling point, enabling the quantification of spatial association patterns at the community scale without mapping individual positions.

Hummock-scale species associations

At the hummock scale, we established two 20 × 2 m transects (T5M and T6M) and recorded all hummocks present (n = 170) (Fig. 1). For each hummock, sampling was conducted vertically from the base—at the water table—up to the canopy, dividing the profile into horizontal layers. Each hummock was approximated as a cylinder, and its total

surface area and volume were estimated from measurements of radius (r) and height (h) using the formulas: $A = 2\pi r(r + h)$ and $V = \pi r^2 h$. These estimates provided the approximate surface area corresponding to each substrate layer. Within each layer, we recorded the non-vascular species forming the substrate and the vascular species rooted in it. The vertical position of each vascular plant was classified into discrete height intervals to detect fine-scale zonation patterns along the hummock gradient.

Functional classification of vascular species by dispersal syndrome

To explore the mechanisms underlying aggregated vegetation patterns, vascular plant species were classified into three functional groups based on their dispersal modes: anemochory, zoochory, and hydrochory. These syndromes were treated as functional traits influencing each species' capacity for colonization and establishment in patchy environments (Soons et al. 2017). Classifications were derived from published floras (Cuatrecasas 1943; Rangel-Ch 2000), global and regional trait databases (Díaz et al. 1999; Kattge et al. 2020), and empirical studies of tropical alpine vegetation (Cleef 1983; Sklenář and Balslev 2007). When species-level information was lacking, genus-level inference and seed morphology were used. Additional literature on Andean dispersal ecology helped resolve ambiguous cases (Tovar et al. 2020). This functional grouping enabled us to test whether variation in species richness was partly driven by dispersal filtering, complementing the model-based evaluation of facilitative processes (Soons et al. 2017).

Environmental variables

Microclimatic monitoring

Temperature and relative humidity were recorded every 30 min over a 12-days period using four HOBO dataloggers (models Micro Station H21, MX2302, and U12-006 with TMC6-HD sensors) installed along the vertical profile of a 60-cm-tall representative hummock. Sensors were positioned at four strata corresponding to dominant plant layers: the basal layer dominated by *Sphagnum cuspidatum* (Sphcus-Basal, < 20 cm; HOBO U12-006), the lower interior by *S. magellanicum* (Sphmage-Interior, 20–40 cm; HOBO H21), the upper interior by *Frullania convoluta* (Frullcon-Interior, 40–60 cm; HOBO H21), and the canopy by *Chusquea tessellata* (Chutess-Canopy, >60 cm; Micro Station H21). Due to limited equipment availability, monitoring was conducted on a single hummock encompassing all target substrates. To compensate for the lack of spatial replication, sensors were left in place for an extended period, allowing for high-resolution temporal characterization of vertical microclimatic gradients within the hummock.

Nutrient content analysis

Composite substrate samples ($n = 5$ per species; total $n = 25$) were collected from five dominant moss species: *Sphagnum cuspidatum*, *S. magellanicum*, *Kurzia capillaris*, *Breutelia squarrosa*, and *Frullania convoluta*. Total carbon (Ct) was measured using the Walkley–Black method, total nitrogen (Nt) by the Kjeldahl procedure, and phosphorus (P) and potassium (K) after calcination. All analyses were performed at the Water and Soils Laboratory of the National University of Colombia (CIER).

Water retention and infiltration rate

To assess moisture regulation by mosses, four samples per species were collected using plastic cylinders (5 cm in diameter × 5 cm in height). The infiltration rate was determined by applying water at a constant rate and recording the percolation time. Water retention was estimated from the difference between dry and saturated weights after oven-drying (160 °C for 110 min) and rehydration with 50 ml of water in airtight bags.

Statistical analysis

To examine the potential relationship between vascular and non-vascular plant richness, we first applied a chi-square (χ^2) test of independence. This test assumes independence among observations—a condition that may be violated in spatially structured ecological data—but was used here as an initial exploratory tool. The analysis was motivated by the framework of Verdú and Valiente-Banuet (2007, 2008), who proposed that significant non-random co-occurrence patterns, when interpreted within an ecological context, can provide evidence of underlying facilitative processes.

At the peatland scale, observed frequencies were used to construct a contingency table with plant species as rows and microsite types (hummocks and valleys) as columns. Expected frequencies were obtained as the product of the total number of individuals and the proportional cover of each microsite type. Species with expected counts < 5 were grouped as "rare species." Significant positive or negative associations were identified through standardized residuals (|Res| >2), indicating departures from independence (Greig-Smith 1983; Valiente-Banuet and Verdú 2007). The same procedure was applied at the hummock scale, using a contingency table in which vascular plant species were related to the dominant moss species with which they co-occurred.

To identify the drivers of vascular plant richness within hummocks, we fitted generalized linear models (GLMs) and generalized linear mixed models (GLMMs) with a Poisson error distribution and a log link function. Vascular species richness was the response variable, and predictors included non-vascular richness, hummock structure (height, area, number of moss layers), soil nutrient content, and microclimatic variation (temperature and humidity ranges). Transect ID was included as a random effect to account for spatial non-independence among sampling points within the same transect. Models were implemented using the *glmer* function in the *lme4* package in R. To reduce multicollinearity, separate principal component analyses (PCAs) were performed for structural, nutrient, and microclimatic variables. The first principal component (PC1) from each analysis was retained as a composite predictor representing structural complexity, nutrient enrichment, and microclimatic stability, explaining 65.5%, 70.7%, and 95.3% of the total variance, respectively (Table S1). Because PCA components are orthogonal by definition, this approach removed collinearity without loss of information. Temperature and relative humidity were expressed as ranges (difference between daily maxima and minima), where wider ranges indicated harsher conditions and narrower ranges reflected more stable microclimates. Variance Inflation Factors (VIF) were all below 7, and most below 2.5, confirming acceptable levels of collinearity even with interaction terms. All predictors were therefore retained to preserve ecological interpretability and comparability across models (Zuur et al. 2009).

To test alternative hypotheses about the factors driving vascular plant richness, we developed eight candidate models representing increasing levels of ecological complexity. The null model (Model 0) contained only the intercept. Additive models (Models 1–3) examined the independent effects of non-vascular richness and hummock structure (height and area), as well as their combined influence. Interaction models (Models 4–6) evaluated whether the effect of non-vascular richness changed with hummock structure, representing potential size-dependent facilitation. Model 7 tested whether facilitation was contingent on microclimatic stability (e.g., temperature and humidity oscillations). In contrast, Model 8 reversed the response variable to assess the potential reciprocal effect, that is, whether vascular richness and hummock structure also explained non-vascular richness. Model performance was compared using the corrected Akaike Information Criterion (AICc) and log-likelihood (logLik) values. For each model, ΔAICc was calculated relative to the best-fitting model to determine relative support. The statistical significance of predictors and interaction terms was evaluated with Wald z-tests ($\alpha = 0.05$). Full model specifications are provided in Supplementary Table S2. All analyses were performed in RStudio (RStudio Team 2024).

Results

Peatland structure and species composition

The studied páramo peatland exhibits a marked microtopography characterized by elevated hummocks and adjacent valleys. Hummocks are dominated by *Sphagnum magellanicum* and underlain by a structural framework of *Chusquea tessellata*, a bamboo typical of high Andean ecosystems. Valleys are covered with mats of *Kurzia capillaris* and *Sphagnum cuspidatum*, the latter being the only species found to persist in permanently waterlogged conditions. This microtopographic configuration suggests the presence of vertically stratified niches, shaped by hydrological gradients and the physical architecture of moss-dominated mounds (Fig. 2). We propose this vertical differentiation as a defining structural feature of páramo peatlands, with distinct biotic assemblages occupying contrasting moisture and nutrient regimes within a small spatial scale.

Across the study area, we recorded 65 plant species. Plant cover reached 91%, and mosses represented 41.5% of the total species richness. Although hummocks covered only 29% of the sampled surface, they hosted 89% of the total individuals and 54% of all species, illustrating their ecological importance. Within hummocks, *Sphagnum magellanicum* (384 counts) and *Breutelia squarrosa* (160) were particularly abundant. Among vascular plants, shrubs were the most frequent biotype (15.4%), followed by tussock-forming grasses (9.2%) and cushion plants (6.2%). The most abundant species overall was the grass *Calamagrostis bogotensis* (1,293 counts), followed by *Chusquea tessellata* (840), the rosette *Puya cryptantha* (432), and the fern *Melpomene flabelliformis* (427), each dominating distinct microhabitats (Supplementary Table S6). *C. tessellata* occurred in every sampled hummock, suggesting a key role in the formation and maintenance of peatland structure. The entire assemblage comprising mosses, liverworts, lichens, ferns, lycopods, orchids, and angiosperms reflects the high structural and taxonomic complexity typical of these Andean wetlands.

Spatial associations with hummock microhabitats

A strong aggregation of species in hummock microhabitats was detected (Fig. 3). A chi-squared test revealed significant deviation from expected distributions ($\chi^2 = 11{,}091.77$, $p < 0.001$). Specifically, 4,618 individuals were observed in hummocks—well above the expected 1,330—while

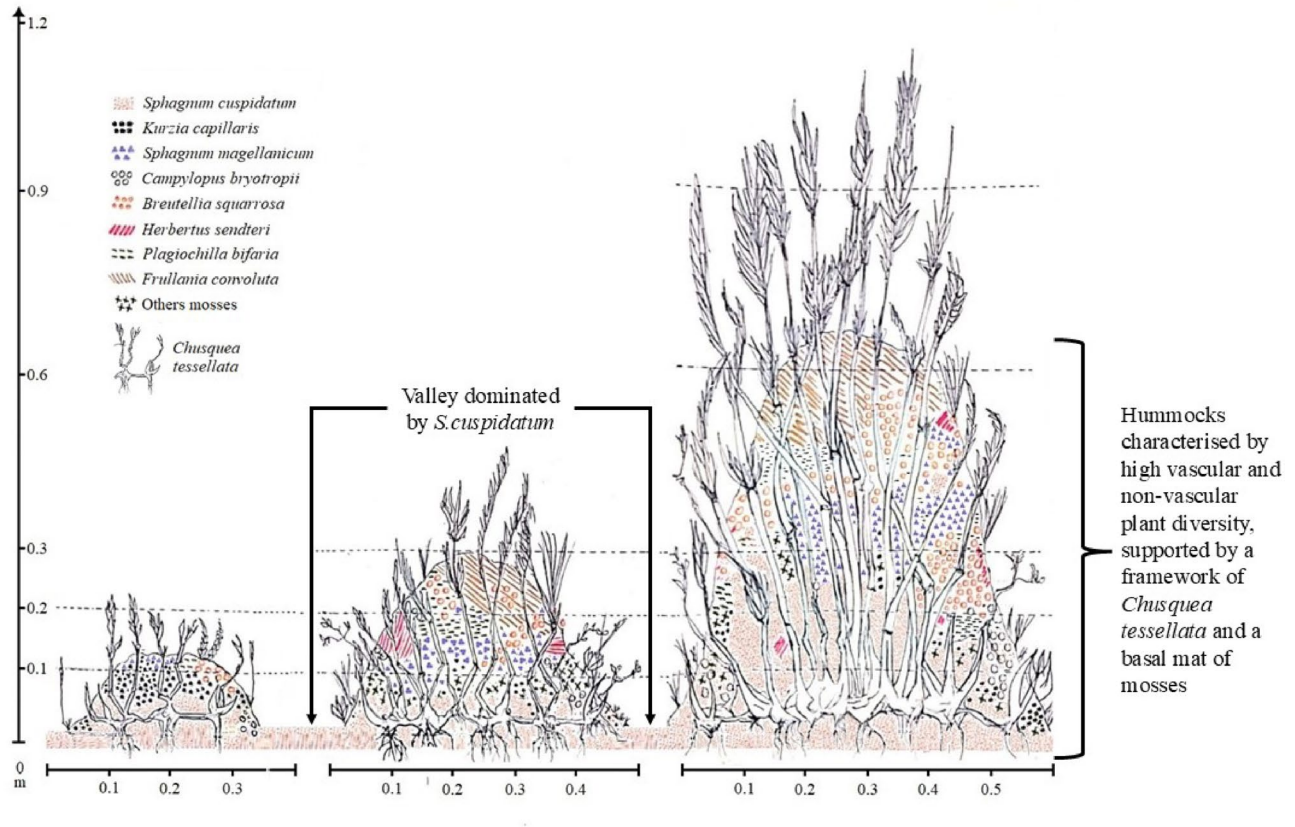


Fig. 2 Schematic representation of three hummocks of increasing size (left to right) and the intervening valleys. Valleys are dominated by *Sphagnum cuspidatum*, while hummocks host diverse vascular and non-vascular assemblages rooted in a basal mat of mosses and *Chusquea tessellata*. Vertical and horizontal axes indicate height and surface distance (m), respectively

only 750 individuals were found in valleys, far below the expected 3,986 (Supplementary Table S3). Standardized residuals confirmed that nearly all species exhibited significantly positive spatial associations with hummocks and negative associations with valley microhabitats, particularly those dominated by *Sphagnum cuspidatum* (Supplementary Table S3). These results support the hypothesis that species are not randomly distributed across the peatland, and instead exhibit strong microhabitat preferences, possibly driven by biotic interactions or differential abiotic filtering.

Hummock-scale species associations

Within the 170 hummocks, we recorded 47 plant species (54.4% vascular, 45.6% non-vascular) and 5,299 species co-occurrences. Potential facilitator species (all non-vascular plants occurring on hummocks) were associated with every vascular plant species recorded and with 98.8% of the 5,299 vascular plant individuals sampled. Contingency table analysis identified nine non-vascular species with potential facilitative roles: *Sphagnum cuspidatum*, *S. magellanicum*, *Kurzia capillaris*, *Campylopus bryotropii*, *Fuscocephaloziopsis crassifolia*, *Breutelia squarrosa*, *Plagiochila bifaria*, *Herbertus sendneri*, and *Frullania convoluta* (Fig. 4, Supplementary Table 4). These species were associated with 100% of the vascular species and 98.8% of all individuals recorded in hummocks. The chi-squared test indicates this pattern is not explained by chance ($\chi^2 = 4397.96$, $p < 0.001$). Given their frequency and widespread presence, *Sphagnum magellanicum*, *S. cuspidatum*, *K. capillaris*, and *Breutelia squarrosa* emerged as key structural and functional species in hummock development and diversity maintenance.

The analysis of significant positive associations (StaRes > 2) revealed that vascular species were not evenly distributed across non-vascular substrates but rather concentrated on a subset of potential facilitators. The tussock-forming grass *Calamagrostis bogotensis* and the shrub *Pernettya prostrata* exhibited strong associations with *Sphagnum cuspidatum*, *S. magellanicum*, and *Kurzia capillaris*, suggesting a preference for mosses capable of maintaining high moisture availability and potentially enriched nutrient conditions. Rosette-forming species such as *Puya cryptantha* were more frequently associated with *Kurzia capillaris* and *Sphagnum* spp., substrates known to accumulate organic matter and increase cation exchange capacity. Epiphytic ferns (*Melpomene flavelliformis*) and forbs (*Geranium*

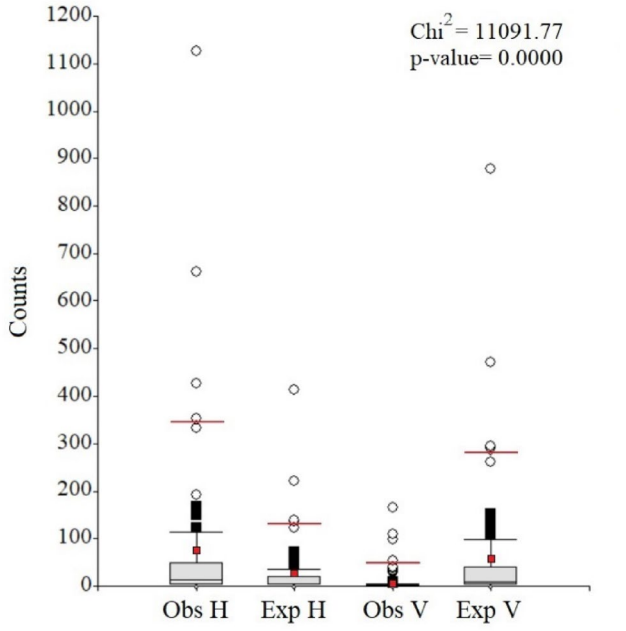


Fig. 3 Distribution of observed (Obs) and expected (Exp) individuals under Hummock (H) and Valley (V) conditions. Hummocks support a diverse assemblage of up to 64 species, whereas valleys are primarily dominated by a single taxon, *Sphagnum cuspidatum*. The red squares indicate the mean, and the red line represents the 95th percentile (Q95)

lainzii, *Gentianella corymbosa*) also showed preferential occurrence on *Breutelia squarrosa* and *Plagiochila bifaria*, which form dense mats that may improve substrate stability and intercept particulate organic inputs. These patterns suggest that vascular species are non-randomly distributed in relation to non-vascular hosts, likely reflecting differences in microhabitat quality linked to substrate identity.

Facilitation and predictors of vascular richness

Model selection indicated that vascular plant richness in páramo peatland hummocks was best explained by a combination of biotic and abiotic factors (Fig. 5; Supplementary Table S5). Although interaction terms showed relatively small effect sizes, models including them received comparable AICc support (ΔAICc < 2) (Burnham & Anderson 2004), suggesting that these effects capture biologically relevant patterns rather than statistical noise. We therefore interpret them as evidence of subtle, size-dependent facilitation, where the influence of non-vascular richness on vascular diversity tends to weaken as hummocks increase in size and environmental stress declines.

Based on AICc comparisons, Models 2, 4, and 5 showed equivalent support (ΔAICc < 2), indicating that vascular plant richness was best explained by the additive and interactive effects of non-vascular richness and hummock structure (area and height). Models with ΔAICc > 10 (e.g., Model 3 and beyond) were not considered in further interpretation. Model 2, the most parsimonious (AICc = 5537.8, df = 6), included non-vascular richness together with hummock height, hummock area, nutrient availability, and microclimate principal components. In this model, vascular richness increased significantly with non-vascular richness (estimate = 0.0886 ± 0.0226, $p < 0.001$), hummock height (0.1764 ± 0.0390, $p < 0.001$), and hummock area (0.1366 ± 0.0456, $p = 0.0027$), while nutrient and microclimate PC1 showed no significant effects ($p > 0.5$). Two interaction models—Model 5 (non-vascular richness × hummock area) and Model 4 (non-vascular richness × hummock height)—also ranked highly (ΔAICc = 0.29 and 1.53, respectively) and retained significant or marginally significant interaction terms. Model 5, although slightly less parsimonious than Model 2, had the highest explanatory power, with strong main effects of non-vascular richness (0.1252 ± 0.0217, $p < 0.001$) and hummock area (0.5464 ± 0.0985, $p < 0.001$), and a negative interaction term (−0.0716 ± 0.0178, $p < 0.001$) indicating that the positive association between non-vascular and vascular richness weakened as hummock area increased. Model 4 revealed a similar, though weaker, interaction when hummock height was considered (non-vascular richness = 0.1180 ± 0.0216, $p < 0.001$; hummock height = 0.3374 ± 0.0773, $p < 0.001$; interaction = −0.0323 ± 0.0166, $p = 0.053$).

Environmental drivers of facilitation

Model 8 was designed to assess whether non-vascular plant richness responds to vascular plant richness, hummock structure, and abiotic conditions (Supplementary Table S5). This model revealed that non-vascular richness increased significantly with hummock height (estimate = 0.085 ± 0.034, $p = 0.013$) and hummock area (estimate = 0.096 ± 0.038, $p = 0.012$), while vascular richness showed a weaker, though still positive, association (estimate = 0.070 ± 0.016, $p < 0.001$). Nutrient availability (Nut_PC1) and microclimate (Clim_PC1) were not significant predictors ($p > 0.63$). These results indicate that non-vascular diversity is primarily driven by hummock size rather than by the diversity of vascular plants, highlighting the asymmetric nature of the relationship between the two groups.

Beyond these environmental correlations, dominant non-vascular species created soils with contrasting nutrient profiles. Substrates beneath *Kurzia capillaris*, *Breutelia squarrosa*, and *Sphagnum cuspidatum* contained higher nitrogen and organic carbon concentrations than those associated with *S. magellanicum* (Fig. 6a). *K. capillaris* had the highest phosphorus levels, while *S. cuspidatum* showed elevated potassium content (Fig. 6a). Significant differences were also detected in hydrological traits among

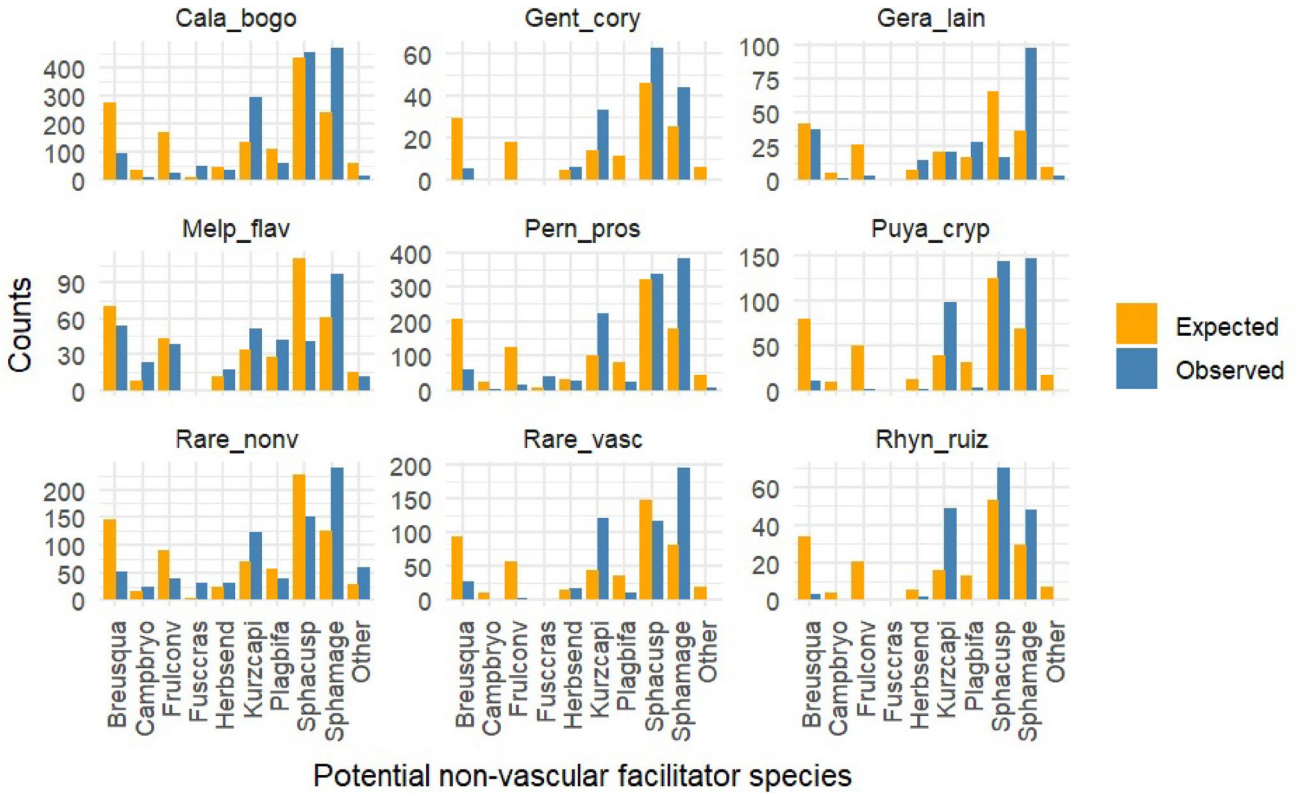


Fig. 4 Observed and expected counts of vascular plant individuals associated with potential non-vascular facilitator species across 170 hummocks. Bars indicate the number of individuals observed in the field (*Observed*, blue) and the counts expected under random association (*Expected*, orange) based on contingency analysis. Only species–facilitator combinations with significant positive associations (standardized residuals > 2) are shown; full results are in Supplementary Table 4. Abbreviations: *Sphagnum cuspidatum* (Sphacusp), *S. magellanicum* (Sphamage), *Kurzia capillaris* (Kurzcapi), *Campylopus bryotropii* (Campbryo), *Fuscocephaloziopsis crassifolia* (Fusccras), *Breutelia squarrosa* (Breusqua), *Plagiochila bifaria* (Plagbifa), *Herbertus sendneri* (Herbsend), *Frullania convoluta* (Frulconv), and other species with less than 50 observed individuals, *Calamagrostis bogotensis* (Cala_bogo), *Pernettya prostrata* (Pern_pros), *Puya cryptantha* (Puya_cryp), *Melpomene flavelliformis* (Melp_flav), *Geranium lainzii* (Gera_lain), *Rhynchospora ruiziana* (Rhyn_ruiz), *Gentianella corymbosa* (Gent_cory), Rare vascular plants (Rare_vasc) y Rare non-vascular plants (Rare_nonv)

moss substrates (infiltration rate: $F = 22.74$, $p < 0.001$; water holding capacity: $F = 4.33$, $p < 0.001$). *K. capillaris*, *S. magellanicum*, and *S. cuspidatum* allowed rapid infiltration, whereas *Fissidens convolutus* and *B. squarrosa* exhibited higher water retention (> 400% of dry weight; Fig. 6b).

Mats of *S. magellanicum* (Sphmage-Interior) retained heat and exhibited elevated nighttime temperatures, suggesting effective thermal buffering. *S. cuspidatum* and *F. convolutus* displayed similar, though less pronounced, patterns. In contrast, canopy sensors on *Chusquea tessellata* recorded the widest diurnal temperature ranges (Fig. 6c). Relative humidity at the hummock base remained near saturation, but *F. convoluta* experienced higher variability than *S. magellanicum*. At canopy level, relative humidity dropped markedly at midday, with fluctuations exceeding 20% (Fig. 6d), supporting the importance of microclimatic stabilization in moss-dominated substrates.

Wind dispersal dominance and Moss-Driven aggregation

Species-level classification revealed that anemochory was the predominant dispersal syndrome among vascular plants, accounting for 71.1% of the species, followed by zoochory (15.7%) and hydrochory (13.3%) (Supplementary Table S6). These findings suggest that the dominant dispersal mode in the study system is wind.

Discussion

Our findings indicate that hummocks constitute structurally elevated microsites above the waterlogged peat surface, thereby providing conditions more suitable for plant establishment than the surrounding inundated matrix. This vertical differentiation explains why, although they occupy only 29% of the peatland area, hummocks host 89% of all recorded individuals and more than half of the species.

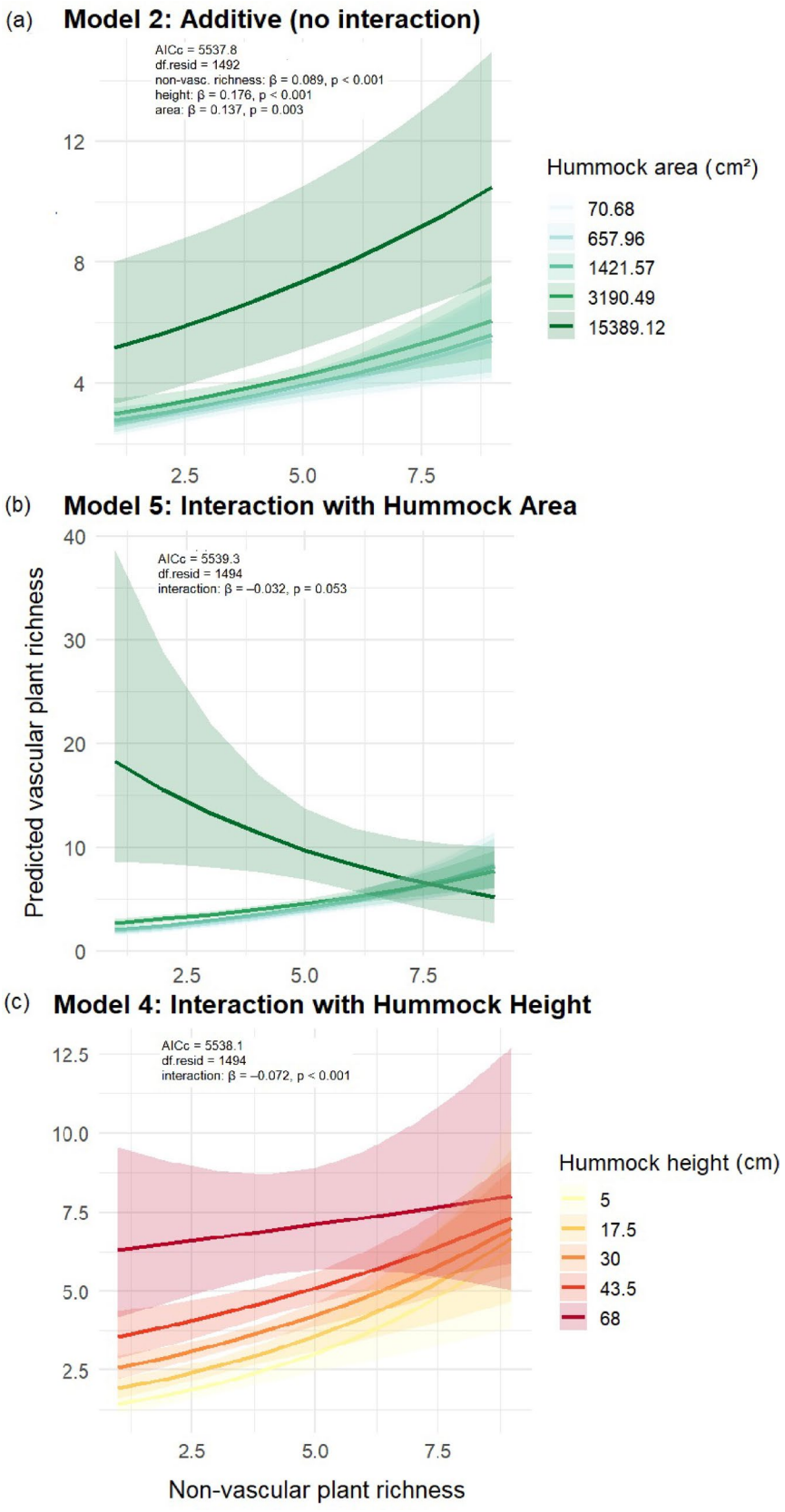


Fig. 5 Predicted effects of non-vascular plant richness and hummock structural attributes on vascular plant richness in páramo peatland hummocks, based on the three best-supported GLMMs (Poisson, log link; random intercept for hummock ID). (a) Model 2 – most parsimonious additive model including non-vascular richness, hummock height, hummock area, nutrient PC1, and microclimate PC1 (AICc = 5537.8, df.resid = 1492); non-vascular richness, hummock height, and hummock area were all significant positive predictors ($p < 0.01$). (b) Model 5 – interaction model including non-vascular richness × hummock area (AICc = 5539.3, df.resid = 1494); the interaction was marginally significant ($p = 0.053$), indicating a size-dependent weakening of facilitation with increasing area. (c) Model 4 – interaction model including non-vascular richness × hummock height (AICc = 5538.1, df.resid = 1494); the interaction was highly significant ($p < 0.001$), with facilitation effects strongest in shorter hummocks. Shaded ribbons represent 95% confidence intervals

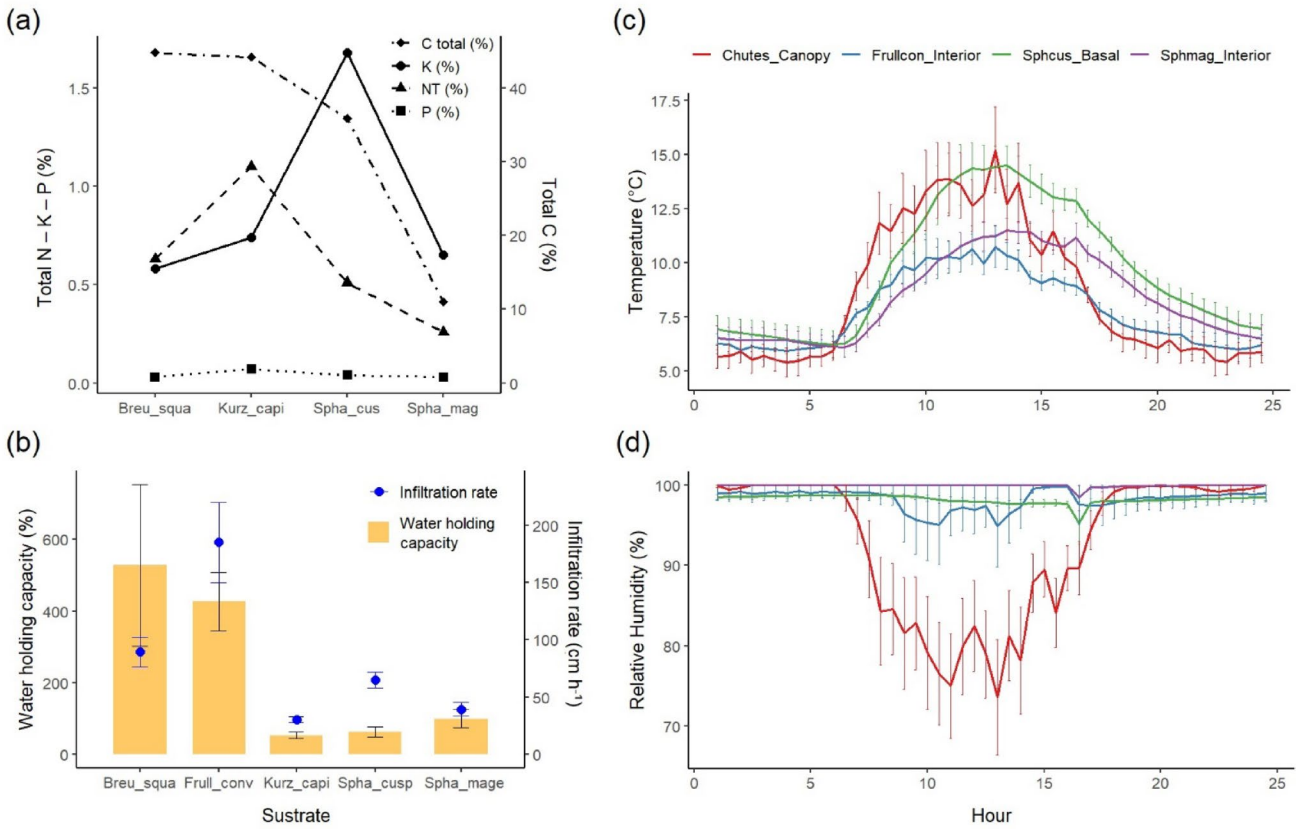


Fig. 6 Abiotic properties of peatland hummock substrates and vertical microclimatic profiles. (a) Percentage of total carbon (% total C), total nitrogen (% total N), total phosphorus (% total P), and total potassium (% total K) in four peatland substrates based on composite samples ($n=5$). (b) Water holding capacity (%) and infiltration rate (cm h^{-1}) of hummock-forming substrates: *Breutelia squarrosa* (Breu_squa), *Kurzia capillaris* (Kurz_capi), *Sphagnum cuspidatum* (Spha_cus), and *Sphagnum magellanicum* (Spha_mag). (c) Mean daily temperature (°C) and (d) relative humidity (%) over 12 days, showing mean hourly values ± standard deviation across four vertical microhabitat levels within the hummock: basal layer dominated by *S. cuspidatum* (Sphcus-Basal, < 20 cm), lower interior by *S. magellanicum* (Sphmage-Interior, 20–40 cm), upper interior by *Frullania convoluta* (Frullcon-Interior, 40–60 cm), and canopy by *Chusquea tessellata* (Chutess-Canopy, > 60 cm). Letters in (a) and (b) indicate results of Fisher's LSD test ($\alpha=0.05$); means sharing the same letter are not significantly different ($p>0.05$)

Within these raised patches, non-vascular mats form the physical foundation of the community by stabilising the substrate, retaining moisture, and accumulating organic matter and nutrients. Together, these processes maintain hummocks as buffered microhabitats that support seedling establishment and long-term plant persistence. The clear spatial aggregation of species within hummocks suggests that their composition is not random but shaped by reciprocal biotic and abiotic interactions, where mosses, liverworts, and vascular plants jointly sustain suitable microenvironments that facilitate coexistence. Species such as *Sphagnum cuspidatum*, *S. magellanicum*, and *Kurzia capillaris* appear to play a central role, modifying hydrological regimes, enhancing nutrient availability, and contributing to the structural integrity of the hummock.

The observed patterns also reveal an asymmetric relationship between plant groups: vascular plant diversity increased significantly with non-vascular richness, whereas non-vascular diversity was mainly influenced by hummock size and remained independent of vascular richness. This asymmetry suggests that mosses and liverworts function as pioneer foundation species, initiating colonization and shaping key physical and chemical conditions, regulating water balance, nutrient availability, and temperature stability to create the microenvironments required for vascular plant establishment. As described by Hunter and Aarssen (1988) and Bruno et al. (2003), such effects represent a form of niche modification consistent with successional dynamics observed in páramo peatlands (Cleef 1981; Schmidt-Mumm & Vargas Ríos, 2012; Silva et al., 2023), where early bryophyte mats set the stage for subsequent vascular colonization. Rather than simply providing habitat, non-vascular plants actively mediate hydrological and nutrient processes that sustain vascular diversity.

Species composition patterns support this interpretation: vascular taxa with higher nutrient demands occurred

disproportionately in moss-dominated hummocks. These distributions suggest that bryophyte mats act as microrefugia, buffering vascular plants against desiccation, thermal extremes, and the nutrient scarcity typical of exposed peat surfaces (Glime 2017; Gornall et al. 2011; Rydin and Jeglum 2013). Strong, species-specific associations between vascular plants and particular moss or liverwort substrates suggest facilitation pathways driven by microenvironmental modification. *Sphagnum* spp. and *Kurzia capillaris*, for instance, not only stabilise moisture and temperature regimes but also trap detritus, enhance microbial activity, and enrich the rhizosphere in nutrients (Gotsch et al. 2016; Laine et al. 2021; Turetsky et al. 2012). Such traits are particularly beneficial for water-demanding or nutrient-sensitive species such as *Pernettya prostrata* and *Calamagrostis bogotensis*. Liverwort mats (*Plagiochila bifaria*, *Herbertus sendneri*) and large mosses (*Breutelia squarrosa*) may offer alternative facilitation routes by stabilising the peat surface, reducing erosion, and creating nutrient-rich microsites through interception of organic particles—conditions favourable to shallow-rooted forbs and epiphytic ferns. The floristic selectivity observed here suggests that vascular colonisation is substrate-driven, where the identity of the non-vascular facilitator shapes the composition of vascular assemblages.

In addition, the bamboo *Chusquea tessellata* mightplay a role in providing more than mechanical support to the hummock formation. Its tall, hollow culms suggest a mechanism similar to that proposed for *Phragmites australis* in temperate wetlands, where the Venturi effect promotes wind-driven convection through the stems, enhancing oxygen transport to the rhizosphere (Armstrong et al. 1992). Such a process could alleviate anoxia in waterlogged soils, stimulate aerobic microbial activity, and indirectly favour seedling establishment. Although this mechanism has not yet been tested in páramo systems, it illustrates a possible case of functional complementarity between vascular and non-vascular dominants in sustaining peatland structure and function.

Environmental modulation by mosses

In other peatlands, the microtopographic heterogeneity of hummocks supports niche partitioning among plant species (Gong et al. 2020; Rydin 1993). This suggests that mosses and liverworts create complex microenvironments that facilitate vascular plant colonization: *Sphagnum magellanicum* stabilizes temperature and moisture regimes, while *Kurzia capillaris* and *Breutelia squarrosa* are associated with nutrient-enriched substrates that may enhance seedling establishment, reflecting contrasting facilitation strategies ranging from nutrient sequestration to active rhizosphere enrichment (Heijmans et al. 2001). The association of *K. capillaris*, *B. squarrosa*, and *S. cuspidatum* with higher phosphorus and nitrogen availability suggests a role in nutrient trapping, which could be especially critical under the oligotrophic conditions typical of alpine peatlands (Albinsson 1997; Hooper 1981).

Beyond nutrient enrichment and thermal buffering, species differ in their ability to regulate water dynamics. Vertical stratification within hummocks creates fine-scale gradients in infiltration and moisture retention that influence plant zonation (Glime 2017; Proctor 2000). This suggests that upper-layer bryophytes, such as *Frullania convoluta* may collect fog or dew, increasing water inputs during dry periods (Glime 2017; Proctor 2000), while basal mosses like *K. capillaris* and *Sphagnum* spp. exhibit high field capacity, effectively retaining rainwater and runoff (Berrones et al. 2024; Montenegro et al. 2005).

Across all top-ranked models, non-vascular richness consistently emerged as the strongest positive predictor of vascular richness, even when structural (hummock size) and abiotic (nutrients and microclimate) variables were included. This supports the view that mosses and liverworts act as nurse species by enhancing moisture retention, stabilizing substrate, and contributing to nutrient accumulation in extreme Andean environments (Gavini et al. 2020; Llambí et al. 2021; Smith 1984). Although interaction terms were weak, the model accounting for the joint effect of hummock area and non-vascular richness suggests that facilitative effects may be size-dependent: strongest in smaller or shorter hummocks and likely to weaken as structural complexity itself buffers microclimatic extremes. This pattern aligns with findings from alpine systems, where facilitation intensity tends to decline as environmental stress decreases (Callaway et al. 2002; Cavieres and Badano 2009; Hacker and Gaines 1997).

The absence of significant nutrient and microclimate effects suggests that, within observed ranges, abiotic differences among hummocks are secondary to structural and biotic drivers. As in other environments colonized by mosses, Sphagnum-dominated mats can decouple plant communities from direct abiotic constraints (Gavini et al. 2020), indicating that microsite structure and local interactions override broader environmental gradients (Anthelme et al. 2014; Cavieres et al. 2014; Llambí and Rada 2019). Likewise, non-vascular richness did not respond significantly to microclimatic variation, consistent with the strong buffering capacity of moss mats in alpine and subalpine wetlands (Carlsson and Callaghan 1991; Gornall et al. 2011; Rydin and Jeglum 2013). This decoupling has also been observed in high-latitude Andean systems, where non-vascular carpets create stable, humid microhabitats that support diverse plant assemblages (Gavini et al. 2020; Llambí et al. 2021; Perez 1987; Zimmer et al. 2018).

Facilitation–competition dynamics in Andean peatlands

Although our results emphasize facilitative effects, it is important to recognize that facilitation and competition frequently co-occur in ecosystems, where their balance shifts along environmental gradients (Callaway and Walker 1997). In ombrotrophic peatlands, which rely entirely on atmospheric inputs for water and nutrients, as is the case in páramo systems, *Sphagnum* species act as major fixers of carbon and nitrogen, giving them a strong competitive advantage over vascular plants that must grow under acidic, nutrient-poor conditions (Aldous 2002). Moreover, *Sphagnum* can retain nitrogen within senescent tissues and later remobilize it through translocation, limiting nutrient release into the surrounding environment (Aldous 2002). Consequently, while coexisting with vascular species, *Sphagnum* often dominates in nutrient acquisition, as vascular plants rely on slower nutrient mineralization processes (Hájek and Adamec 2009). Competition also arises among Sphagnum species themselves: hummock-forming taxa such as *S. magellanicum*, can exclude hollow-dwelling species like *S. cuspidatum*, which harbour a diverse microflora of nitrogen-fixing algae and cyanobacteria that confer advantages under permanently waterlogged conditions (Bu et al. 2013; Hájek and Adamec 2009). Conversely, when moisture declines and water becomes limiting, hummock species suppress hollow species (Bu et al. 2013). These contrasting interactions highlight that moss–vascular coexistence emerges from a dynamic balance between facilitation and competition, where microtopographic and hydrological gradients mediate the relative strength of each process.

Dispersal vs. facilitation

The predominance of wind-dispersed species suggests a stochastic, non-directional dispersal regime, typical of open alpine ecosystems (Cavieres and Arroyo 2001). Under such conditions, the arrival of propagules at suitable microsites is random mainly, and species aggregation would not be expected without reinforcement by local filtering mechanisms. In contrast, hydrochory—though less common—can produce directed seed deposition along moisture gradients, as observed in wetland systems (Soons et al. 2017). However, its low representation in our data indicates a minor role in shaping vegetation patterns. In such stochastic dispersal contexts, successful establishment depends heavily on habitat modification, corroborating the role of moss-mediated facilitation in generating the strong, non-random clustering of vascular plant richness observed in moss-dominated hummocks. By buffering environmental stress and modulating abiotic conditions, mosses enhance the likelihood that arriving propagules can germinate and persist, thereby linking dispersal processes with community assembly outcomes.

Future directions

Our findings confirm that moss-mediated facilitation is a key driver of community structure in Andean peatlands, yet important knowledge gaps remain. Research should explore how facilitative effects vary seasonally, how fog interception contributes to water balance, and how nutrient fluxes fluctuate over time. Experimental studies assessing moss responses to environmental change will be essential for designing effective restoration strategies under future climate scenarios. Comparative analyses across different páramo peatlands could also reveal whether the patterns observed here are system-specific or broadly applicable, providing a stronger basis for regional conservation planning.

Conclusion

The patterns observed in this Andean peatland demonstrate that hummocks harbour disproportionately high species richness and abundance despite their limited spatial extent. This study contributes a novel perspective by integrating environmental and structural variables, moving beyond traditional floristic inventories to better understand the spatial and ecological organization of these systems. Our models reveal that non-vascular plant richness, more than environmental variables or hummock size, best explains vascular plant diversity, emphasizing the central role of ecological facilitation. Vertical zonation within hummocks reflects functional differentiation: basal species such as *Sphagnum cuspidatum* and *Kurzia capillaris* are associated with higher nutrient concentrations, while the middle and upper strata, dominated by *Sphagnum magellanicum*, *Frullania convoluta*, and *Breutelia squarrosa*, regulate temperature and moisture dynamics. *S. magellanicum* acts as a thermal buffer, and *F. convoluta* and *B. squarrosa* enhance water retention, particularly during the dry season when fog is the primary moisture source. Together, these findings show that mosses facilitate the establishment and persistence of companion species by improving microhabitat conditions. This facilitative effect shapes plant community structure and contributes directly to the biodiversity and resilience of high-mountain peatlands.

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Author contributions Liz Ávila-Rodríguez and Alfonso Valiente-Banuet conceived the ideas; Liz Ávila-Rodríguez, Alfonso Valiente-Banuet, and Tania Sánchez-Ortiz designed the methodology and collected the data; Liz Ávila-Rodríguez, Tania Sánchez-Ortiz, Alfonso Valiente-Banuet, and Miguel Martínez-Ramos analysed the data; Liz Ávila-Rodríguez and Clara Tinoco-Ojanguren led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data availability The datasets generated and analyzed during the current study are available from the corresponding author upon reasonable request.

Declarations

Competing interests The authors declare no competing interests.

Ethical approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

Clinical trial number not applicable.

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