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Plant dispersal strategies of high tropical alpine communities across the Andes

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Abstract

1. Dispersal is a key ecological process that influences plant community assembly. Therefore, understanding whether dispersal strategies are associated with climate is of utmost importance, particularly in areas greatly exposed to climate change. We examined alpine plant communities located in the mountain summits of the tropical Andes across a 4,000-km latitudinal gradient. We investigated species dispersal strategies and tested their association with climatic conditions and their evolutionary history.

2. We used dispersal-related traits (dispersal mode and growth form) to characterize dispersal strategies for 486 species recorded on 49 mountain summits. Then we analysed the phylogenetic signal of traits and investigated the association between dispersal traits, phylogeny, climate and space using structural equation modelling and fourth-corner analysis together with RLQ ordination.

3. A median of 36% species in the communities was anemochorous (wind-dispersed) and herbaceous. This dispersal strategy was followed by the barochory-herb combination (herbaceous with unspecialized seeds, dispersed by gravity) with a median of 26.3% species in the communities. The latter strategy was common among species with distributions restricted to alpine environments.

4. While trait states were phylogenetically conserved, they were significantly associated with a temperature gradient. Low minimum air temperatures, found at higher latitudes/elevations, were correlated with the prevalence of barochory and

the herb growth form, traits that are common among Caryophyllales, Brassicaceae and Poaceae. Milder temperatures, found at lower latitudes/elevations, were associated with endozoochorous, shrub species mostly from the Ericaceae family. Anemochorous species were found all along the temperature gradient, possibly due to the success of anemochorous Compositae species in alpine regions. We also found that trait state dominance was more associated with the climatic conditions of the summit than with community phylogenetic structure. Although the evolutionary history of the tropical Andean flora has also shaped dispersal strategies, our results suggest that the environment had a more predominant role.

5. *Synthesis*. We showed that dispersal-related traits are strongly associated with a gradient of minimum air temperatures in the Andes. Global warming may weaken this key filter at tropical alpine summits, potentially altering community dispersal strategies in this region and thus, plant community structure and composition.

1 | INTRODUCTION

Dispersal plays a key role in species local survival (Clobert, Baguette, Benton, & Bullock, 2012), plant community assembly (Howe & Westley, 1996) and gene flow within and between populations (Matthysen, 2012). Plant dispersal is particularly relevant for alpine species because their habitats are naturally fragmented (Flantua, O'Dea, Onstein, Giraldo, & Hooghiemstra, 2019) and have undergone increased fragmentation due to land-use change (Spehn, Liberman, & Körner, 2006; Tovar, Duivenvoorden, Sánchez-Vega, & Seijmonsbergen, 2012). Not only new habitat configuration but changes in environmental conditions, due to ongoing climate change (Vuille et al., 2018), could make dispersal less effective for certain species, thus affecting community assembly, particularly at high elevations (Zimmer et al., 2018). However, whether plant dispersal strategies are associated with the climate remains understudied in tropical alpine regions, hindering our ability to assess how they may be affected by climate change.

Plant dispersal strategies involve different key traits (Bonte et al., 2012). One of the key ones is dispersal mode, which depends on the diaspore (part of the plant that is dispersed) morphological structures. For example, seed wings or pappi favour dispersal by wind (anemochory), edible fruits are dispersed by animals that eat them (endozoochory), hooks attach to animals' fur (epizoochory) and seeds without morphological adaptations rely on dispersal by gravity (barochory; van der Pijl, 1982). Animal-dispersed seeds achieve longer dispersal distances than those dispersed by wind and those without morphological adaptations (Tamme et al., 2014). Other traits such as growth form and plant height also play a role in determining dispersal distances as diaspores of taller species achieve longer dispersal distances than shorter ones (Tamme et al., 2014; Thomson et al., 2010). Although other traits such as seed mass and seed terminal velocity might play a role on species

dispersal as well, dispersal mode and growth form enable reasonable predictions of dispersal distances to be made (Tamme et al., 2014).

Under the trait-based ecology framework (Enquist et al., 2015), traits are expected to reach optimal values (trait states) under a specific climate condition. However, in many parts of the world, such as tropical alpine systems, dispersal trait–environment relationships remain little understood. Previous studies suggested that certain growth forms are better adapted to lower minimum temperatures (Arzac, Llambí, Dulhoste, Olano, & Chacón-Moreno, 2019; Carilla et al., 2018; Halloy & Mark, 1996; Hedberg & Hedberg, 1979). However, trait–environment studies of dispersal mode in alpine regions show some mixed results. In the Swiss Alps, decreasing temperatures along the elevation gradient correlate with an increased proportion of plant species whose seeds have pappus (except at the limit of plant growth in nival areas; Pellissier, Fournier, Guisan, & Vittoz, 2010). In the northern Andes (11°N–6.5°S), a decrease in the importance of epizoochorous species and an increase of anemochorous species along the elevation gradient has been shown (Frantzen & Bouman, 1989; Melcher, Bouman, & Cleef, 2000). However, no correlation is found between the presence of pappose seeds and elevation in the Apennines (Di Musciano et al., 2018) or the Tibetan Plateau (Qi et al., 2014) nor between herbaceous species adapted to zoochory and elevation. The contrasting patterns could result from the differences in elevation and latitudinal ranges included in each study. Therefore, a comprehensive regional analysis of traits related to dispersal along environmental gradients is needed in alpine regions to elucidate potential associations with climate.

In addition to trait–environment relationships, traits within a given community are expected to be influenced by macroevolutionary patterns (Gerhold, Cahill, Winter, Bartish, & Prinzing, 2015). Closely related species could have inherited similar traits from a common

ancestor, which is defined as phylogenetic conservatism (Cadotte & Davies, 2016). For example, traits related to reproduction such as flowering and fruiting phenology show strong phylogenetic conservatism in alpine meadow communities (Li et al., 2016). It is therefore essential to explore the effect of phylogenetic relatedness on dispersal-related traits observed in alpine communities (de Bello et al., 2015).

The Andes exhibit climatic gradients linked to elevation and latitude that strongly influence the patterns of its alpine plant community assemblages (Cuesta et al., 2017). One hypothesis (H1) that may explain the composition of dispersal-related traits in these alpine communities is that harsher climatic conditions at the coldest summits could filter out some dispersal-related traits and favour others. In support for H1, growth forms seem to be constrained by climatic conditions in tropical alpine regions (Arzac et al., 2019; Hedberg & Hedberg, 1979) and dispersal mode and elevation seem to be associated in some temperate alpine regions (Pellissier et al., 2010). However, the tropical Andean summits studied here were relatively recently colonized in the last 4–12 Ma, when the largest mountain building of the Andes occurred (Hoorn et al., 2010). Therefore, a second hypothesis (H2) is that dispersal traits were inherited from ancestors that colonized the newly uplifted areas and phylogenies are driving dispersal trait composition in high Andean communities. In support for this, it has been suggested that taxa with high radiation in the Andes first colonized newly uplifted environments without morphological innovations, driven by ecological opportunities offered by a new habitat and the absence of competition (Hughes & Atchison, 2015; Hughes & Eastwood, 2006).

The aim of this paper is to investigate the association between dispersal strategies (by using the dispersal-related traits, that is, dispersal mode and growth form), climate and evolutionary history (phylogenetic relatedness) in mountain summits of the tropical Andes (>3,200 m) across 4,000 km of latitudinal gradient. The main objectives are: (a) to characterize plant dispersal strategies of high Andean species and communities, (b) to assess the association of plant dispersal strategies with current climatic conditions (H1) and evolutionary history (H2). As these are not mutually exclusive hypotheses, here we analysed whether H1 or H2 are predominantly associated with dispersal traits within communities for our second objective. While

the association between dispersal traits, climate and phylogenies has been partially explored for montane forest systems of the northern Andes (Buitrón-Jurado & Ramírez, 2014), to our knowledge, no similar study has been conducted in the tropical alpine systems.

2 | MATERIALS AND METHODS

2.1 | Community data

Plant community data (species composition) were recorded between 2012 and 2013 on 49 summits between 3,200 and 5,500 m a.s.l., using 8 to 16 1-m^2 plots per summit (Cuesta et al., 2017) across the Tropical Andes (Figure 1). Our study area covers two major tropical alpine biomes: (a) the paramo, located in the northern Andes, with humid conditions and (b) the puna, located in the Central Andes with drier conditions (location of northern and central Andes, and differences in temperature are shown in Figure 1, further details of our study area are included in the Supporting Information: Methods). These plots are part of the GLORIA-Andes long-term monitoring network and the measurements follow the standard methods developed by the GLORIA global network (Pauli et al., 2015). The warmest summits are located closer to the equator or in sub-alpine habitats closer to the upper forest line (UFL) while the coldest summits are located further from the equator or in sub-nival or nival habitats (Figure 1). For this study, we used the presence/absence data collected in the plots of fully identified seed plants. We summarized subspecies and varieties into parent species' binomial, because dispersal trait data and phylogenetic information were difficult to obtain for lower ranks (see next sections). Finally, we obtained plant community data for a total of 486 species on the 49 summits (Supporting Information: Species list).

2.2 | Trait data

We collected information of two traits associated with plant dispersal strategies, namely dispersal mode and growth form. These

FIGURE 1 Study area showing the 49 summits across the Andes and their air temperatures. (a) Location of the 49 summits in 13 sites across the tropical Andes (Supporting Information: Methods), picture of Pichincha, Ecuador (top) in the northern Andes and picture of Parque Nacional Sajama, Bolivia (bottom) in the central Andes (b) Maximum temperature of the warmest month, annual mean temperature and minimum temperature of the coldest month of the 49 summits across latitude (distance from equator, absolute values of latitude) and elevation (m a.s.l.). Temperatures were extracted from the CHELSA dataset (Karger et al., 2017) for each location and then a smooth was applied
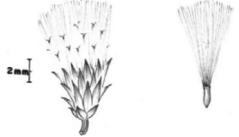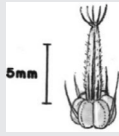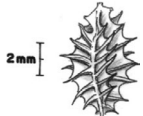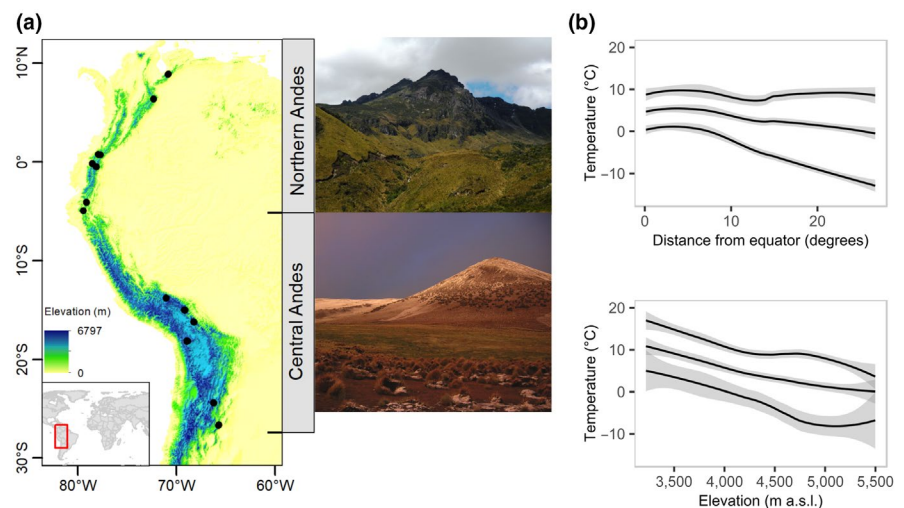
TABLE 1 Description of the dispersal mode categories used in this study. Dispersal modes were assigned based on the morphological adaptations of the diaspore (fruits or seeds). Drawings by Carlos Maldonado

Dispersal mode	Dispersal agent	Morphological adaptations	Example
Anemochory	Dispersed by wind	Balloon seeds (minute seeds with distinct air spaces, typically seed coat with honeycomb pattern)	*Baccharis caespitosa*
		Dust seeds	
		Plumose/hairy seeds/fruits	
		Winged seeds/fruits	
Ballochory	Dispersed ballistically	Ballistic dispersal active explosives (active movements due to high pressure in living cells)	*Geranium sessiliflorum*
		Ballistic dispersal passive explosives (passive (hygroscopic) movements of dead tissues)	
Barochory	Unassisted, gravity	Diaspore without morphological adaptation (unspecialized seeds)	*Arenaria pycnophylla*
		Windballist (long, stiff fruit stalks swung by wind releasing unspecialized seeds through the pores of the fruit)	
Endozoochory	Dispersed by animals (diaspore is ingested)	Edible seeds/fruits/appendages	
Epizoochory	Dispersed by animals (diaspore is carried accidentally)	Straight stiffed appendages as bristles or awns	*Tetraglochin cristatum*
		Hooks	
		Spiny appendages	
		Mucilage	
Hydrochory	Dispersed by water	Air bubbles/floatability	*Azorella multifida*
Other	Clonal, myrmecochory (dispersed by ants), synzoochory (diaspore is carried by animals intentionally, zoochory (without specification of type e.g. endozoochory, ectozoochory, synzoochory)		

traits have been identified as key traits in determining plant dispersal distances (Tamme et al., 2014). Based on the morphology of their diaspores, we assigned each species a dispersal mode: (a) anemochory, (b) ballochory, (c) barochory, (d) endozoochory, (e) epizoochory and (f) hydrochory (Table 1). The information was gathered from the literature and herbarium specimens (Supporting Information: Methods). We identified the dispersal mode for 471 species (96.9% of total species). For the remaining species, given that they lack apparent morphological adaptations, or their congeneric species were mostly barochorous, we assumed these species were barochorous as well (Supporting Information: Methods).

We used four growth form categories: (a) herb, (b) shrub, (c) tree and (d) epiphyte, based on the Tropicos database (www.tropicos. org). This classification was preferred over a more detailed classification of Andean alpine growth forms (e.g. Ramsay & Oxley, 1997) due to data availability and because it matches those used by dispersal studies (e.g. Thomson et al., 2010).

Given that species could have more than one trait category (trait state), we built species versus traits matrix as multi-choice nominal variables for each trait (Pavoine, Baguette, & Bonsall, 2010).

2.3 | Climatic data

In the absence of local climatological data for all our 49 summits, we extracted data from the CHELSA dataset at 30 arc sec resolution (period 1979–2013; Karger et al., 2017). Because Andean precipitation patterns are currently not yet well described, due to its high spatio–temporal variability and the low density of rain gauges (Manz et al., 2016), underestimations and overestimations in precipitation values are expected. We checked Pearson's correlations between the 19 bioclimatic variables and selected the following less correlated combination (Pearson < 0.7, see details in Supporting Information: Methods): (a) maximum temperature of the warmest month, (b) minimum temperature of the coldest month, (c) total annual precipitation and (d) precipitation of the coldest quarter. We chose minimum and maximum temperature over mean annual temperature to capture the thermal extremes for which alpine plants need to adapt (Cavieres, Badano, Sierra-Almeida, Gomez-Gonzalez, & Molina-Montenegro, 2006; Körner, 2003). These extremes are therefore key in structuring high alpine plant communities (Rundell, Smith, & Meinzer, 1994). Minimum temperature was highly correlated with both distance from the equator and elevation (Figure 1).

2.4 | Phylogeny

We used a species-level multi-gene phylogeny from the publicly available database BIEN 2 (http://bien.nceas.ucsb.edu/bien/biendata/bien-2/phylogeny/). The BIEN 2 tree covered 79% of species in our dataset. For species unplaced in BIEN 2 tree (102 species), we grafted each of them by randomly selecting a branch within the clade containing congeneric (or confamiliar when a genus was unplaced) species and then randomly binding a focal species on the branch. By repeating the procedure 1,000 times and comparing the outputs, we confirmed that the random grafting was not influential in the evaluation of phylogenetic community structure and climatic correlations (Supporting Information: Methods). We used the R package BIEN (Maitner et al., 2018) to download BIEN 2 tree and APE (Paradis, Claude, & Strimmer, 2004) and PHYTOOLS (Revell, 2012) for editing phylogeny.

2.5 | Statistical analysis

2.5.1 | Characterizing plant dispersal strategies

We analysed the composition of trait states at the species and community level. First, we estimated the percentage of species out of the total species regional pool ($n = 486$) with each dispersal mode and growth form categories. In addition, we classified each species based on their current full distribution range (biogeographic groups) following Cuesta et al. (2020) in seven categories: (a) paramo endemic, (b) puna endemic, (c) tropical Andean alpine (present in both the paramo and the puna), (d) Andean alpine (present in both the tropical and temperate Andes), (e) tropical montane (present above and below the tree line within the tropics), (f) neotropical (present in the Andes and the south American lowlands) and (g) cosmopolitan (present in the neotropics and beyond). Then, we analysed the trait state composition by biogeographic group to identify trait patterns across the geographic distribution of the species.

Second, we analysed the community composition of dispersal strategies (i.e. combination of growth-form and dispersal mode) by estimating for each community the percentage of species with each strategy.

2.5.2 | Phylogenetic signal

We tested the phylogenetic signal of each trait state (i.e. closely related species tend to share more similar trait states than distantly related species) using two statistics: Pagel's λ (Pagel, 1999) and D-statistic (Fritz & Purvis, 2010). For Pagel's λ, values closer to 1 indicate stronger phylogenetic signal while values closer to 0 indicate that a trait state has a weak signal and a random phylogenetic structure. D-statistic values are interpreted inversely of those of Pagel's λ (see details in Supporting Information: Methods). Analyses were run in R using the packages GEIGER (Harmon, Weir, Brock, Glor, & Challenger, 2008) and CAPER (Orme et al., 2018).

2.5.3 | Association between plant community, traits, phylogeny and climate

We first conducted piecewise structural equation modelling (piecewiseSEM) to test the hypothesized association between the dominance of trait states within communities, the climate and the community phylogenetic structure. A piecewiseSEM model was built for each particular trait state by using the percentage of species with that trait state in each community. Because of the relatively small number of samples (number of communities = 49), we selected two climatic variables (minimum temperature and total annual precipitation) to minimize the number of explanatory variables. These variables were chosen because of their importance as limiting physiological factors for alpine plant species (Cavieres et al., 2006; Körner, 2003) and their values varied the most across our sites. As a measure of community phylogenetic structure, we calculated phylogenetic species variability (PSV) for each community, which represents the degree to which species are phylogenetically related (Helmus, Bland, Williams, & Ives, 2007). PSV varies from 0 (minimum variability, high species relatedness) to 1 (maximum variability, low species relatedness). We also accounted for number of species to control the effect of species richness on the functional structures. In the piecewiseSEM analysis, we incorporated three linear regression models: the first and second models explain species richness and PSV by the two climatic variables, respectively; a third model explains the dominance of functional trait by species richness, PSV and the climatic variables. In the regression, we also accounted for spatial structure of the sampling communities as a site-dependent random effect by dividing 49 communities into four site groups based on geographical position (i.e. north/south of the northern and central Andes). The goodness-of-fit of the piecewiseSEM model was evaluated by Fisher's C statistic (Shipley, 2000). We used the R package PIECEWISESEM (Lefcheck, 2016) for conducting the piecewiseSEM analysis, NLME (Pinheiro, Bates, DebRoy, Sarkar, & R Development Core Team, 2019) for fitting linear regression model with a random effect and PICANTE (Kembel et al., 2010) for calculating PSV.

Secondly, we applied the multivariate version of the fourth-corner analysis developed by Pavoine, Vela, Gachet, de Bélair, and Bonsall (2011) to test the significance of (a) trait–climate relationship across communities, (b) phylogeny–climate relationship across communities, (c) trait–geographical space relationship across communities (traits are structured spatially) and (d) phylogeny–geographical space relationship across communities (phylogenies are structured spatially). We used four different matrices: summit x climate (C: climatic conditions in each summit), summit × summit (S: spatial distance between summits), species × traits (T: traits of all species), species × species (P: phylogenetic distances between all species) that are linked by a species × summit matrix (L: presence/absence of species in each summit). The fourth-corner analyses test the significance of the connection between C × S and T × P matrices by comparing it against null models (species across the tips of the phylogenetic tree were permuted). After testing the significance of the connections between matrices, the RLQ ordination can relate them

graphically to observe the relationships (see details in Supporting Information: Methods). Analysis were run in R using the codes provided by Pavoine et al. (2011).

Lastly, as a way to infer whether trait states are constrained by climatic conditions we analysed if species with different dispersal mode/growth form had, in average, different thermal responses. We obtained the thermal optimum, minimum and maximum for each species from Cuesta et al. (2020). These values were built using monthly temperatures extracted from all known locations of the species (whole distribution range). Then we tested for differences in thermal optimum, minimum and maximum between species with different trait states using the Games-Howell post-hoc test that accounts for differences in sampling size.

3 | RESULTS

3.1 | Plant dispersal strategies and trait phylogenetic signal

The most common dispersal mode among our 486 species and within communities was anemochory (209 species and a median of 45.8% species within communities), followed by barochory (unspecialized seeds that disperse by gravity, 164 species and a median of 27.7% of species within communities; Figures S3a and S4a). The dominance of dispersal modes varied between communities (Figure S4b). Most of the species were herbaceous and this growth form was also dominant within communities (Figures S3b and S4a).

The most common dispersal strategy (combination of trait states) within communities was anemochory-herb, used by a median of 36% species (Figure 2) and barochorous herbaceous species represented a median of 26.3% within communities. Nearly 50% of the anemochorous species and 30% of herbaceous species belonged to Compositae (Figure S5).

When analysing dispersal mode by biogeographic group we found that the tropical montane biogeographic group had the highest proportion of endozoochory, the puna endemic group had the highest proportion of anemochory and the Andean alpine group had the highest proportion of barochory (Figure S6). In all biogeographic groups, the dominant growth form category was herbaceous. All trait states showed a phylogenetic signal (Table 2).

3.2 | Association between plant community, traits, phylogeny and climate

3.2.1 | Piecewise structural equation modelling

First, the piecewise structural equation modelling analysis showed that colder summits were associated with higher PSV (low species relatedness) than summits with milder climatic conditions (Figure 3). Second, minimum air temperature and annual precipitation had a stronger correlation with the dominance of trait states within plant communities than phylogenetic relatedness (Figure 3). The dominance of endozoochory, hydrochory, barochory, and the growth forms herb, shrub and tree was correlated with the environment. Only the dominance of epizoochory and barochory was correlated with PSV. Community percentages of anemochorous species (Figure 3) and epiphytes (results not shown) did not have any significant correlation either with climate or with PSV.

Higher percentage of endozoochorous species was found in warmer summits, while higher percentage of barochorous and hydrochorous species was associated with colder conditions. The model for hydrochory dominance had a strong spatial structure (marginal R^2 is very low, indicating most of its variance was
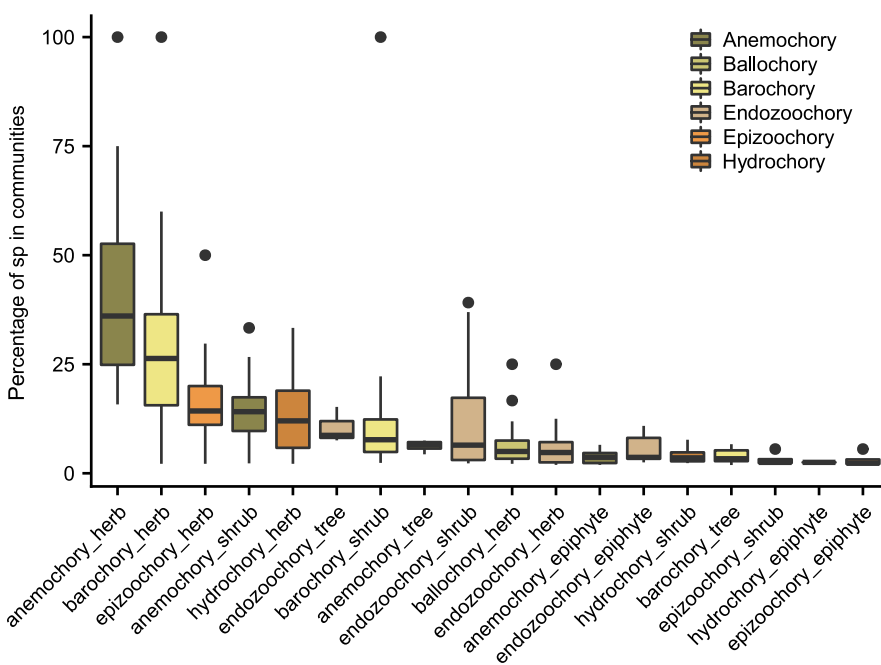

FIGURE 2 Community plant dispersal strategies based on the combination of dispersal mode and growth form categories. The graph shows the percentage of species within the 49 communities that have the dispersal strategy

TABLE 2 Phylogenetic signal analysis for each trait state of dispersal mode and growth form using Pagel's λ and the *D*-statistic (see Section 2). BM = Brownian motion model, prob. = probability, prob. dif. = probability of differ from

	Pagel's λ			*D*-statistic			Phylogenetic pattern	
Trait state	Estimated λ	Prob. dif. random structure	Prob. dif. BM phylo structure	Estimated *D*	Prob. random structure	Prob. BM phylo structure	Interpretation lamda (λ)	Interpretation *D*
Dispersal mode								
Ballochory	1	<0.001	1	−0.346	0	0.952	Clumped BM	Extremely clumpled
Endozoochory	0.999	<0.001	1	0.041	0	0.393	Clumped BM	Clumped BM
Anemochory	0.979	<0.001	1	0.124	0	0.070	Clumped BM	Clumped
Barochory	0.988	<0.001	1	0.212	0	0.011	Clumped BM	Clumped
Hydrochory	0.884	<0.001	1	0.353	0	0.016	Clumped BM	Clumped
Epizoochory	0.880	<0.001	1	0.413	0	0	Clumped BM	Clumped
Growth form								
Tree	0.994	<0.001	1	0.229	0	0.162	Clumped BM	Clumped BM
Herb	0.967	<0.001	1	0.301	0	0	Clumped BM	Clumped
Shrub	0.957	<0.001	1	0.322	0	0	Clumped BM	Clumped
Epiphyte	0.880	<0.001	1	0.598	0	0.010	Clumped BM	Clumped

FIGURE 3 Path diagrams explaining community trait percentages in relation to the following fixed variables: minimum temperature of the coldest month (minT), total annual precipitation (pp) and community phylogenetic structure (phylogenetic species variability = PSV) for dispersal mode and growth form categories. A site-dependent random variable was incorporated to account for potential spatial autocorrelation (see Section 2). Only diagrams with significant correlations between FS and environmental variables or PSV are shown. FS is the percentage of each functional state in the community. R^2 in brackets are the marginal R^2 (i.e. ration of variance explained by fixed variables). SR, sp richness.
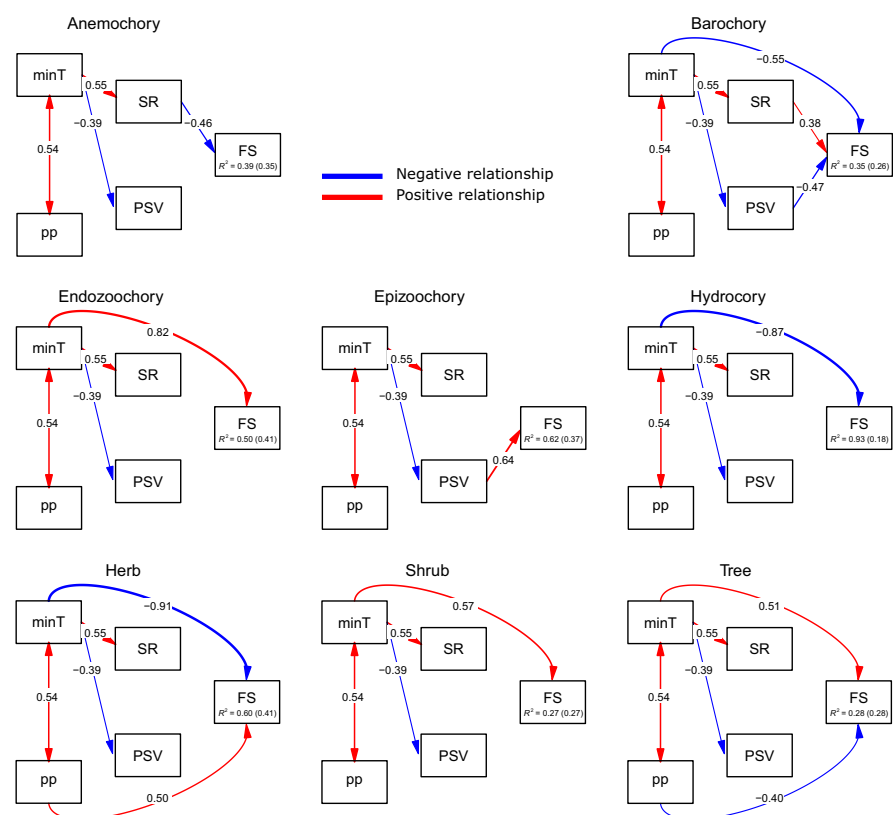
explained by spatial structure). Barochory was also higher in communities with lower PSV (high species relatedness) while higher epizoochory was recorded in communities with higher PSV (low species relatedness). Higher anemochory was found in species-poor communities which in turn was influenced by lower minimum air temperatures.

Lastly, community percentages of different growth form states were only associated with climatic conditions and not with PSV. While communities with higher percentage of shrub and tree species were associated with higher minimum air temperatures, communities with higher number of herbaceous species were associated with colder summits, as expected.

3.2.2 | Fourth-corner tests and RLQ ordination analysis

The fourth-corner tests showed a significant association be-tween our two dispersal traits (dispersal mode and growth form)
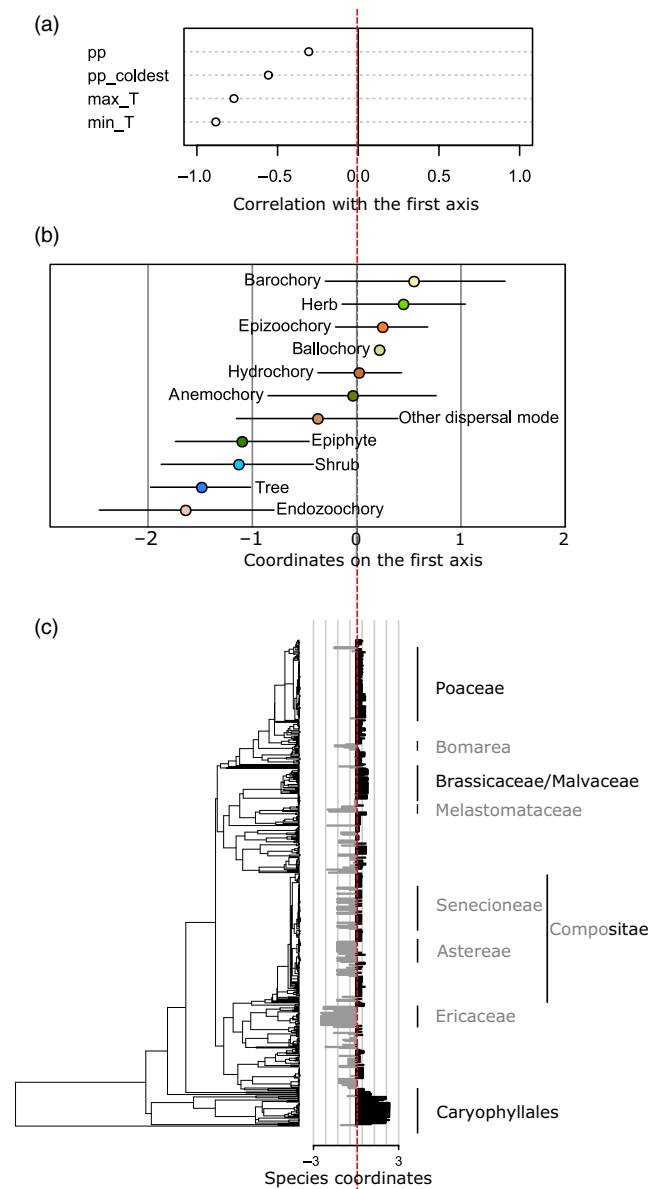

(a)

(b)

(c)

FIGURE 4 RLQ ordination results using the first axis.
(a) Pearson correlations between the climatic variables (total annual precipitation = pp, precipitation of the coldest quarter = pp_coldest, maximum temperature of the warmest month = max_T, minimum temperature of the coldest month = min_T) and the RLQ coordinates of the summits on the first axis. (b) Trait states are located at the average coordinates of the species that possess them. The length of the segment represents the standard deviation of the scores. (c) Phylogeny and coordinates of the species. Higher minimum and maximum temperatures (left side of [a]) were associated with trait states in the left side of (b) and with taxa in grey bars in the left side of (c). Lower minimum and maximum temperatures (right side of [a]) were associated with traits and taxa in black bars on the right side of the figures in (b) and (c) respectively

and the climate ($p = 0.001$ for both), and between traits and space ($p = 0.001$ for both traits). Phylogenies were significantly associated with the climate ($p = 0.03$), but no association was found with space ($p = 0.53$).

The first axis of the RLQ ordination analysis explained 73.3% of the variance and represents a gradient dominated mainly by temperature and to a lower extent by precipitation (Figure 4a). The second axis explained 8.9% and was mostly driven by precipitation where the presence of hydrochorous species was higher in wet-ter summits (Figure S7). The first axis of the trait ordination plot showed that the presence of species with unspecialized seeds (ba-rochory) and mostly herbaceous growth form were associated with colder summits (Figure 4b). Thesme trait states are characteristic of Brassicaceae, Malvaceae, Poaceae and Caryophyllales (Figure 4c) which are common elements at the colder summits. In contrast, the presence of endozoochorous species and tree and shrub spe-cies was associated with warmer summits. These trait states are common among the shrub families Ericaceae and Melastomataceae (Figure 4c).

Ballochory, anemochory and hydrochory were located in the middle of the first axis, indicating no preference for a particular part of the temperature gradient. For example, in the case of Compositae where most species are anemochorous, herbaceous species were
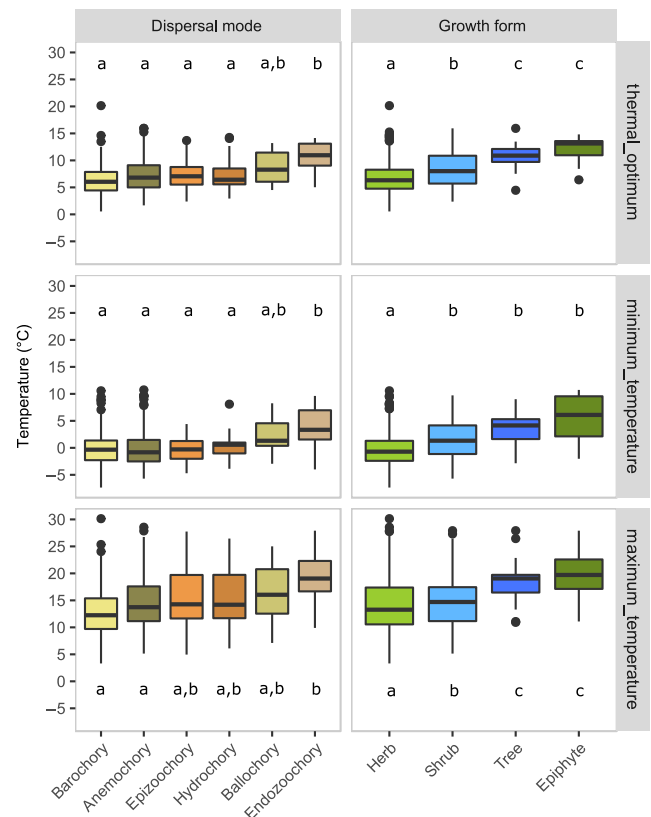

FIGURE 5 Comparison of thermal optimum, minimum and maximum temperature between species with different trait states. Different letters represent a significant difference between biogeographical species groups ($p < 0.05$) based on Games–Howell test

associated with colder summits while shrub species (mainly from the subfamilies Senecioneae and Astereae) were associated with milder climatic conditions (Figure 4c).

3.2.3 | Dispersal-related traits versus species thermal responses

Endozoochorous species had statistically significant higher thermal optima and minima than species with other dispersal modes, except for ballochory, but only differed from barochorous and anemochorous species in terms of thermal maxima (Figure 5). We found that herbs had the lowest thermal responses, followed by shrubs and trees (although the difference between shrubs and trees was not significant for minimum temperature). Epiphytes had similar thermal responses as trees (Figure 5).

4 | DISCUSSION

4.1 | Plant dispersal strategies in the high tropical Andes

The predominant dispersal strategy in plant communities across high Andean summits was the combination of trait states anemochory-herb, closely followed by the barochory-herb combination (Figure 2). Different dispersal strategies have an impact on dispersal distances (Tamme et al., 2014; Thomson et al., 2010). For example, anemochorous shrub species (e.g. *Baccharis obtusifolia*, *Valeriana microphylla)* are expected to have longer dispersal distances than anemochorous herbaceous species (e.g. *Erigeron rosulatus*, *Pycnophyllum molle*) due to the higher seed release height of shrubs in comparison with that of herbaceous species. A better estimation of dispersal capacity could be obtained if seed release height is used (Tamme et al., 2014; Thomson et al., 2010), therefore further studies should collect this information for tropical alpine species.

Dispersal capacity of anemochorous species also depends on the trade-offs between the size of the flying apparatus (appendages) and seed size (Halloy, 1989). Further studies are needed to better understand these trade-offs along elevation gradients because atmospheric density decreases with increasing elevation, making air seed lift more difficult (Halloy, 1989; Körner, 2003).

In contrast to the dominance of anemochory in the high Andes, European alpine summits and Asian alpine regions are dominated by species with unspecialized seeds (Bu et al., 2008; Di Musciano et al., 2018; Matteodo, Wipf, Stöckli, Rixen, & Vittoz, 2013). This difference might be explained partially by the higher number of Compositae species in South America than in Europe (Panero & Crozier, 2016) that are predominantly dispersed by wind (Figure S5). Below we discuss the association of dispersal strategies with both climate and evolutionary history in the Andes, to better understand these strategies.

4.2 | Climate is strongly associated with plant dispersal strategies in mountain summits

Dispersal traits were strongly associated with climatic conditions across mountain summits in the tropical Andes, supporting our first hypothesis (H1). First, when analysed together, dispersal mode and growth form categories were arranged along a temperature gradient. Second, when analysed separately, most trait states showed a stronger correlation with climate than with phylogenetic relatedness.

Along the alpine temperature gradient (Figure 4a,b), the prevalence of endozoochorous shrub species, mostly belonging to the Ericaceae family (Figure S5), decreased from summits with milder temperatures to colder summits (i.e. from lower latitudes/elevations to higher latitudes/elevations). This is in agreement with what was found along a latitudinal gradient in Australia (10°N–45°S; Chen, Cornwell, Zhang, & Moles, 2017) where higher temperatures closer to the equator were a strong predictor of endozoochory. A positive correlation between percentage of endozoochorous species and temperature was also found for the montane forests of the northern Andes (Buitrón-Jurado & Ramírez, 2014) but no relationship with temperature has been found when studying montane and lowland forest together (Correa, Álvarez, & Stevenson, 2015). These contrasting results could be due to different trait–environment relationships in lowland and montane forests, but this has yet to be tested. A potential explanation for the limited presence of endozoochorous shrub species in the coldest environments is the high costs involved in producing suitable pulp for dispersers (Bonte et al., 2012; Buitrón-Jurado & Ramírez, 2014).

At the coldest summits, the presence of herbaceous barochorous species was higher. While seeds are most likely to remain closer to the parents and avoid the risks of arriving to unsuitable habitats, this strategy increases the risk of kin competition (Matthysen, 2012; Starrfelt & Kokko, 2012). On the other hand, interspecific competition could be lower in highly stressful environments, such as colder summits, where facilitation mechanisms may prevail (Callaway et al., 2002). In fact, several of our barochorous species (e.g. *Gentiana sedifolia*) seem to benefit from nurse species such as *Azorella aretioides* or *Arenaria musciformis* that promote higher moisture and soil organic matter in their neighbourhood (Anthelme, Buendia, Mazoyer, & Dangles, 2012; Hupp, Llambí, Ramírez, & Callaway, 2017). This facilitation could partially explain the success of the barochorous herbaceous strategy in cold conditions, however, more research is needed to understand the importance of kin competition from species with this strategy.

Anemochorous species showed high success across the temperature gradient. One reason for this is that anemochorous herbaceous species are associated with a ruderal life strategy (Grime, 1977) that makes them good colonizers (Sarmiento, Llambi, Escalona, & Marquez, 2003). These species do not only thrive in soils with low fertility (Spasojevic, Damschen, & Harrison, 2014) and areas with open canopy (Ozinga, Bekker, Schaminee, & Van Groenendael, 2004), but also in well-established soils (Matteodo et al., 2013). In the high

tropical Andes, anemochory prevailed in species-poor communities (Figure 3), which could be linked to incipient soil development on steep slopes (Cuesta et al., 2019). Thus, soil development and type may better explain the dominance of anemochorous species rather than temperature.

The dominance of most trait states was associated more to climatic conditions than to phylogenetic relatedness. Three growth categories out of four were associated with climate and not with phylogenetic relatedness, while three of six dispersal mode categories were associated to climate and only two with phylogenetic relatedness (Figure 3). Also, communities located in the coldest summits were formed by less phylogenetically related species than sub-alpine communities or those located closer to the equator. All this suggests that environmental filtering potentially becomes more prevalent as minimum temperatures become more limiting, reducing, for example, the presence of endozoochorous shrubby species in the coldest summits.

Because the limited presence of particular dispersal strategies could result not only from environmental constraints but other factors (Kraft et al., 2015), we also analysed the thermal responses of species with different trait states. We used the entire distribution range of each species to estimate the thermal responses instead of only the community data in the 49 studied summits. We found that, indeed, endozoochorous shrub species had significantly higher thermal optima, minima and maxima than barochorous, anemochorous and epizoochorous species that are herbaceous. This potentially indicates that endozoochorous shrub species were limited by the environment. However, to properly test this, it might be necessary to carry out transplanting experiments (Kraft et al., 2015). Although observational data are not perfect, they can provide useful information on environmental filtering (Cadotte & Tucker, 2017) and our results suggest that climatic constraints had a predominant role in shaping dispersal strategies in the high Andes.

4.3 | The role of evolutionary history

Although dispersal strategies of high Andean flora were strongly associated with climatic conditions, they were also associated with its evolutionary history, giving partial support to our H2. Similar trait states were most likely to be found among closely related species than among distantly related species (Table 2), indicating that trait states, in many cases, were inherited from ancestors (H2). However, we also found that phylogenies were associated with climate (Figures 3 and 4) but not with space, indicating that certain phylogenetic groups have specific preferences for specific climates irrespectively of geographic location. One example of the combined effect of phylogeny and climate in determining dispersal strategies is the genus *Espeletia*, endemic to the northern Andes. The absence of pappi in *Espeletia's* seeds, inherited from their ancestor, may have contributed to their restricted distribution in the coldest parts of the northern Andes and the high endemism within the group (Pouchon et al., 2018). More broadly, the

Compositae family underwent a major radiation in the Andes at around 30 Ma (Panero & Crozier, 2016), resulting in the presence of several genera across the tropical Andes. The rapid radiation has been hypothesized to be related not only with the dispersal success due to the pappus but with whole genome duplication, a phytomelanized fruit that seems to protect seeds from herbivory (Panero & Crozier, 2016) and a ruderal strategy that allowed them to colonize newly uplifted regions (Halloy, 1983). These successful traits in Compositae, may help explain the dominance of anemochory across our tropical alpine summits irrespectively of temperature.

4.4 | Implications for climate change scenarios and future steps

Given that plant dispersal strategies of the high Andean flora were associated with a temperature gradient, warming scenarios could lead to a change in these at the community level. A recent study in Andean sites that have been gradually deglaciated since the 1970s, found that anemochory dominated the newly established plant communities (>90%; Zimmer et al., 2018). But, over time, anemochorous species slowly decreased in number at the oldest sites in the chronosequence, while zoochory increased from 0% to 6%. The endozoochorous species in our study have tropical montane, neotropical and cosmopolitan distributions and have higher thermal optima than species with other dispersal modes (Figure S6; Figure 5). These characteristics could help endozoochorous species to eventually outcompete cold-adapted species such as the barochorous herbaceous species under warming scenarios. Cold-adapted species also have narrower thermal niches (Cuesta et al., 2020) and are typical of biomes projected to suffer habitat reduction due to climate change (Tovar, Arnillas, Cuesta, & Buytaert, 2013). A reduction in species with unspecialized seeds has been already observed in European mountain summits during the last century due to warming (Matteodo et al., 2013), highlighting the potential risk to the Andean barochorous species due to climate change.

In order to complement our findings about dispersal and the risk of climate change, future studies should focus on seedling establishment under climate change scenarios. These should include both observational and experimental approaches, specially to determine the extent to which safe site availability controls vegetation dynamics (e.g. Llambí, Puentes Aguilar, & García-Núñez, 2013). Also, more studies are required to explore clonality of tropical alpine species, which is another very common way of reproduction in European alpine species (Körner, 2003), but very little information exists about clonality for the tropical Andean species.

AUTHORS' CONTRIBUTIONS

C.T., F.C., I.M. and A.C. conceived the ideas and designed the methodology; C.T., I.M. and R.I.M. collected the trait data; C.T. and B.K. analysed the data; F.C., R.I.M., S.H., L.D.L., S.B., P.M., R.J., J.J. and J.C. coordinated/participated in the collection of the community data in the GLORIA-Andes summits; P.M. and F.C. curated the taxonomic and community data; C.T. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Species trait data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.xksn02vc8 (Tovar et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.