Global Ecology and Conservation 59 (2025) e03537

Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: www.elsevier.com/locate/gecco

Original research article

Phylogenetic diversity and structure above the tree line in the central Chilean Andes in the light of competing macroecological hypotheses

Ítalo Tamburrino [a,b,c,*], Mary T.K. Arroyo [a,b,c,*], Paola Jara-Arancio [b,c,d]

[a] *Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, Las Palmeras, Ñuñoa 3425, Chile*
[b] *Cape Horn International Center (CHIC), O'Higgins 310, Puerto Williams, Chile*
[c] *Instituto de Ecología y Biodiversidad (IEB), Las Palmeras, Ñuñoa 3425, Chile*
[d] *Departamento de Ciencias Biológicas y Departamento de Ecología y Biodiversidad, Facultad de Ciencias de la Vida, Universidad Andrés Bello, República 440, Santiago, Chile*

ARTICLE INFO

Keywords:
Phylogenetic structure
Spatial scale
Phylogenetic resolution
Alpine
Andes

ABSTRACT

The “Tropical Niche Conservatism” (TNC) and “Out of the Tropics” (OTT) hypotheses were developed originally in relation to latitudinal species richness gradient. To determine whether the predictions of these theories play out across elevational gradients in the central Chilean Andes, we determined species richness (SR), Relative Phylogenetic Diversity (PD_{SES}), Mean Pairwise Distance (MPD_{SES}) and Mean Nearest Taxon Distance ($MNTD_{SES}$) at 100 m elevational intervals for five plot sizes over two above tree line gradients embedded in the same regional flora. We assessed the effect of phylogenetic resolution using two species-level phylogenies resolved to different degrees. After an initial gradual increase followed by a gradual decline, both SR and PD decreased with elevation. $MNTD_{SES}$ transitioned from phylogenetic overdispersion in the subalpine to clustering in the upper alpine with unclear elevational trends at the smaller spatial scales. Results for MPD_{SES} were equivocal. Although results for the two phylogenies were closely correlated, lower phylogenetic resolution favored decreased site-level PD at all spatial scales and a trend in the direction of phylogenetic overdispersion for PD_{SES} and $MNTD_{SES}$ at the smaller spatial scales. Overall, TNC provides a more coherent explanation for our results in the Chilean Andes than OTT. Lower SR and lack of phylogenetic clustering at lower elevations on the two gradients are attributed to contingencies of the Miocene uplift of the Andes leading to a more arid climate and depressed treeline. Spatial scaling effects call for well resolved species-level phylogenies in studies seeking to relate phylogenetic structure to local ecological effects. However, the degree of phylogenetic resolution becomes less critical when the focus is on broad macroecological trends.

1. Introduction

Biodiversity is unevenly distributed latitudinally across the globe with a clear tendency for fewer species at higher colder latitudes (Gaston, 2000; Hillebrand, 2004). Analogously, in concert with decreasing temperature, species richness tends to decline with

---

[*] Corresponding authors at: Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, Las Palmeras, Ñuñoa 3425, Chile.
E-mail addresses: italo.tamburrino@ug.uchile.cl (Í. Tamburrino), southern@uchile.cl (M.T.K. Arroyo).

https://doi.org/10.1016/j.gecco.2025.e03537
Received 13 November 2024; Received in revised form 18 February 2025; Accepted 10 March 2025

elevation (Guo et al., 2013). Uplifted mountain ranges have a parallel in the late Eocene-induced steepening of the global temperature gradient in that mountain building has been associated with a progressive reduction in air temperature. Understanding the distribution of biodiversity, including species richness and phylogenetic diversity and structure over the latitudinal and altitudinal gradients is of great theoretical interest. It is also relevant when it comes to the conservation of biodiversity where an important objective is to maximize lineage coverage (Faith, 1992).

Two contrasting theories have emerged regarding phylogenetic structure along the latitudinal gradient. The "Tropical Niche Conservatism" (TNC) hypothesis posits major clades diversified and expanded rapidly under warmer Early Cretaceous global temperatures (Qian and Ricklefs, 2016; Wiens and Donoghue, 2004). As global temperatures began to fall as of the late Eocene, most tropical lineages were forced to withdraw from higher latitudes because of strong phylogenetic niche conservatism. Phylogenetic niche conservatism is supported by closely related species tending to share the same niche or biome (Crisp et al., 2009; Peterson et al., 1999; Wiens et al., 2010). Even some major clades, such as the succulent species of *Caesalpinia,* are largely restricted to a single biome (Gagnon et al., 2019). Nevertheless, as global temperatures cooled, a limited number of lineages were able to acquire adaptations enabling them to remain and diversify in temperate climates resulting in clusters of closely related species. According to the TNC hypothesis, clade age generally decreases and the phylogenetic relatedness of species increases with increasing latitude and globally decreasing temperature (Qian and Ricklefs, 2016).

The "Out of the Tropics" (OTT) hypothesis accepts that lineages have mostly originated in tropical environments but were not impeded from surviving in lower latitudes (Jablonski et al., 2006). Higher species richness in present-day tropical regions is attributed to the tropics harbouring a mixture of both old and young taxa and the higher latitudes lacking younger taxa. According to this second hypothesis, mean clade age increases and the phylogenetic relatedness of species decreases with increasing latitude and decreasing temperature (Jablonski et al., 2006).

Arguably, if the above hypotheses are relevant for explaining latitudinal biodiversity trends, they should find support over elevational gradients. Here we focus on phylogenetic diversity and phylogenetic structure over the elevational gradient in above tree line plant communities in the central Chilean Andes. In their seminal study, Qian et al. (2021) showed that above tree line alpine floras tend to exhibit a greater level of phylogenetic clustering than their respective regional floras. However, exactly where clustering occurs along the alpine gradient was not determined. This is critical question. Is the entire alpine gradient clustered in general or is clustering limited to a certain section of the gradient? To answer questions of the kind, detailed gradient studies above treeline are imperative.

The central Chilean Andes, occurring on the western side of the north-south trending Southern Andes, are characterized by exceptionally steep elevational gradients and a strong decline in plant species richness above tree line (Cavieres et al., 2000). Although important autochthonous above tree line radiations are evident (e.g., *Leucheria*, Pérez et al., 2020), the Southern Andes appear not to have experienced direct allochthonous colonization by cold-adapted northern hemisphere clades as occurs in the Northern Andes (Arroyo and Cavieres, 2013; Madriñán et al., 2013; Sklenář et al., 2011). The few important northern hemisphere clades represented above tree line appeared initially in lowland areas (e.g., *Valeriana,*Bell et al., 2012, and probably both clades of *Astragalus*, Scherson et al., 2008). Any increase or decrease in phylogenetic relatedness of species over elevation in the central Chilean Andes thus will strongly reflect the dynamics of regional biogeographic processes during uplift. Above tree line gradients in the central Chilean Andes therefore provide an ideal scenario to examine the effect of elevation per se on community assembly.

To shed light on which hypotheses better explains the community assembly process in the central Chilean Andes, we examined how phylogenetic diversity and phylogenetic structure vary across elevation, from near the tree line to the upper limit of vegetation. We approached this question using vascular plant data for different sized plots obtained in 100 m elevational bands along two gradients. If above tree line communities in this part of the Andes assembled in accordance with the TNC hypothesis, we expect decreasing species richness with elevation to be accompanied by increasingly higher levels of phylogenetic clustering. To the contrary, under the OTT hypothesis, we expect decreasing species richness with elevation to be accompanied by increasingly higher levels of phylogenetic overdispersion. In both cases, the amount of PD is expected to decrease with elevation. However, under the TNC hypothesis, relative PD to the number of species is expected to decrease toward higher elevations, while under the OTT hypothesis it is likely to increase.

Consideration of more than one elevational gradient and continuous sampling across gradients is especially relevant when looking for macroecological trends in mountainous terrain. In highly dissected alpine landscapes, local micro-topographical variation, differences in exposition and soil types are likely to produce deviations from the mainstream expectations of hypotheses like the TNC and OTT over elevation. A practical way to deal with this problem is to search for broad similarities in phylogenetic structure across separate elevational gradients sharing the same regional species pool. For this reason, in this study, we considered two extensive elevational gradients in the same general area that were sampled at 100 m elevational intervals without intermittent gaps.

Sampling units such as plots, when small, are likely to capture a smaller proportion of the total flora in the lower parts of above tree line gradients where species richness tends to be higher than at higher elevations (Cavieres et al., 2000; Cuesta et al., 2023; Shaheen et al., 2023). This could potentially decrease the chances of capturing elevational trends in phylogenetic structure. An important question, therefore, is whether elevational tendencies detected in phylogenetic structure vary according to the size of sampling units. Another relevant question concerns taxonomic resolution. In a continental-scale study based on data for 110 x110 km quadrats, a strong correlation was reported for phylogenetic metrics calculated using well resolved and less resolved phylogenies (Qian and Jin, 2021). However, at relatively small spatial scales, where richness is expected to be lower, differences in the lengths of branches between phylogenies could lead to disproportionate differences in phylogenetic structure. In consideration of the previous and last point, as part of our study, we asked whether the detection of phylogenetic patterns over elevation in our system is affected by the size of sampling units and the level of resolution of the phylogeny used.

2. Methods

2.1. Study area

Work was carried in the central Chilean Andes (33° S) east of the city of Santiago (Fig. 1A). At this latitude the Southern Andes reaches a height of 6070 m a.s.l (Nevado El Plomo) within ca. 50 km of the eastern edge of the central valley. The study area spans the treeless subalpine belt and the complete high alpine belt up to the limit of consistent vascular plant vegetation. Azonal high elevation bogs and other wetlands were not considered. The tree line is comprised of open woodland dominated by the small tree *Kageneckia angustifolia* (Rosaceae). Subalpine vegetation is dominated by low shrubs while "true" alpine vegetation is dominated by large cushion-forming species associated with rosette and low growing perennial herbs and subshrubs. This area of the Andes is characterized by a semi-arid climate with a Mediterranean influence (Di Castri and Hajek, 1976). Mean annual precipitation in the subalpine at 2500 m a.s.l. is 445 mm, ascending to 943 mm at 3200 m a.s.l. (Cavieres et al., 2006). Temperatures recorded at 1.5 m a.g.l. with data loggers (Arroyo et al., 2024) provide an adiabatic lapse rate of −5.9 °C km^{-1}. The mean monthly temperature in the subalpine belt at 2406 m a.s.l. was 9.0 °C descending to 2.3 °C in the upper alpine belt at 3555 m a.s.l. Specifically, we worked in the La Parva and Valle Nevado areas (Fig. 1B). The sites on the La Parva gradient were located between 2576 and 3636 m a.s.l. Those on the Valle Nevado gradient were located between 2346 and 3686 m a.s.l. Uniform and/or undisturbed areas of vegetation sufficiently large to support our sampling design could not be found below 2500 m a.s.l. on the La Parva gradient. Fig. 2 provides a selection of species that appear on our sampling sites.

2.2. Plot data

For the largest plot size, we used data reported in Arroyo et al. (2024). This source provides data on all vascular plants recorded in the 2022–2023 austral summer in one square-shaped 1600 m^2 plot (hereafter, large plots) per each 100 m elevational band on the two gradients (total of 27 sampling stations). Plots on the shorter La Parva gradient (12 sampling stations) cover a lineal distance of 5 km. Those of the Valle Nevado gradient (15 sampling stations) cover a lineal distance of 7.5 km. Sampling sites on the two gradients occurring in the same 100 m elevational band are separated by 1.82–4.48 km (Mean = 3.04 km). Over the 2022–2023 austral summer, we also sampled all vascular plant species for four smaller plot sizes (five 1 m^2, five 25 m^2, one 100 m^2 and one 400 m^2) nested within the large plots with the objective of assessing the effect of plot size on phylogenetic diversity and structure. The 1 m^2 and 25 m^2 plots were located on the four corners of the large plot with a fifth pair located in the center of that plot. One corner of the large plot was then randomly selected to locate the 100 m^2 plot and the 400 m^2 plot which were extensions of that cornerś 25 m^2 plot and 100 m^2 plot, respectively. Including the five plot sizes and the two gradients, data was available for 351 plots. A total of 168 vascular plant taxa (167 species with one species represented by two subspecies) (hereafter 168 species for simplicity) were identified on the 27 sampling sites (Arroyo et al., 2024). Of these, 140 appeared on the Valle Nevado gradient and 127 on the La Parva gradient. The 168 species registered in the plots pertain to 93 genera of which 41 (44.1 %) are represented by more than one species. The three largest genera represented are *Adesmia* (Fabaceae) (8 species), *Nassauvia* (Asteraceae) (5 species) and *Senecio* (Asteraceae) (5 species). Other large

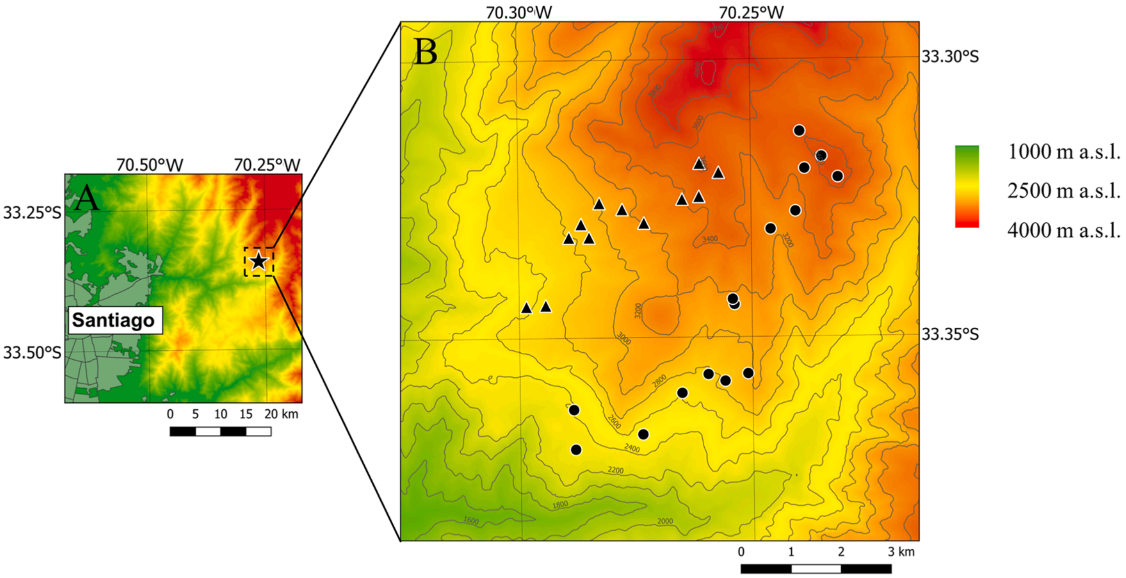

Fig. 1. A. Location of study area (★) in central Chile in relation to the city of Santiago; B. Sampling sites on the La Parva (▲) and Valle Nevado (●) gradients. The sites on the La Parva gradient were located between 2576 and 3636 m a.s.l. Those on the Valle Nevado gradient were located between 2346 and 3686 m a.s.l.

Fig. 2. Selection of species recorded on the sampling sites. A. *Gamocarpha compacta* (Calyceraceae); B. *Azorella ruizii* (Apiaceae), C. *Rhodolirium montanum* (Amaryllidaceae); D. *Tropaeolum nubigenum* (Tropaeolaceae); E. *Tristagma bivalve* (Amaryllidaceae); F. *Chuquiraga oppositifolia* (Asteraceae); G. *Azorella madreporica* (Apiaceae); G. *Oriastrum lycopodioides* (Asteraceae); I. *Viola atropurpurea* (Violaceae); J. *Calandrinia caespitosa* (Montiaceae).

genera are *Acaena* (Rosaceae), *Carex* (Cyperaceae), *Montiopsis* (Montiaceae) and *Poa* (Poaceae), all with 4 species. The complete data set for all plots sizes and elevational bands on the two gradients can be found at https://doi.org/10.17632/jd25sfgxv4.1

2.3. Phylogenetic tree construction

We constructed a phylogeny resolved at the species level (hereafter $\text{PHYLO}_{\text{sp.resolved}}$) using the nuclear marker ITS and the plastid regions, *rbcL* and *matK*. Where sequences were not available in GenBank, DNA was extracted in our laboratory from leaf material collected in the field and stored in silica gel or obtained from herbarium material (see S1 and Table S1 for laboratory protocols and primer details). Overall, 69.6 % of the species counted with usable sequences for the three markers, 25.0 % for two markers and 5.4 % for one marker (see Table S2 for details of sequences and vouchers). For tree construction, Bayesian inference was performed in the CIPRES Science Gateway V. 3.3 Portal (www.phylo.org). *Ginko biloba* (Ginkgoaceae) was chosen as an outgroup. Evolutionary models were: ITS GTR+I+GM; *rbc*L GTR+GMM and *mat*K GTR+G. Model selection was based on the Akaike Information Criterion. Parameters were sampled for 20 x 10^6 generations with 25 % of the first samples discarded. Nodes with ≥ 0.95 were considered robust for posterior probabilities (Ronquist et al., 2012). The effective sample size (ESS) value was greater than 200 in the range of 4540 and 33650 (Tracer program, v1.6; Rambaut et al., 2014)). Sequences were unavailable for an unidentified species of *Trisetum*. In this case, prior to analysis, a branch was added to $\text{PHYLO}_{\text{sp.resolved}}$ at mid distance from the node separating *T. longiglume* from its sister taxon.

To assess the effect of phylogenetic resolution, we generated a second, less resolved phylogeny (hereafter $\text{PHYLO}_{\text{sp.polytomies}}$). One randomly selected species per genus was retained in $\text{PHYLO}_{\text{sp.resolved}}$ to provide a genus-level phylogeny. The pruned species were then replaced by branches attached at mid-distance from the basal node of each genus to represent them as polytomies (as done by Qian and Jin, 2021). The topologies of the two phylogenies are shown comparatively in Figure S1.

2.4. Data analysis

Species richness (SR) and phylogenetic diversity (PD; Faith, 1992) were determined for each plot in both gradients. To detect whether PD deviated from random expectation, Relative PD (PD_{SES}) was calculated (Webb, 2000). For phylogenetic structure, we calculated the standardized effect size of Mean Pairwise Distance (MPD_{SES}) and Mean Nearest Taxon Distance (MNTD_{SES}) (Webb, 2000). PD_{SES}, MPD_{SES} and MNTD_{SES} were calculated as χ_{obs} - $\chi_{\text{null}}/\text{SD}_{\text{null}}$, where χ_{obs} was observed PD, MPD or MNTD, χ_{null} was the mean PD, MPD or MNTD of the 9999 randomizations and SD_{null} was the standard deviation of the simulated values. Randomizations

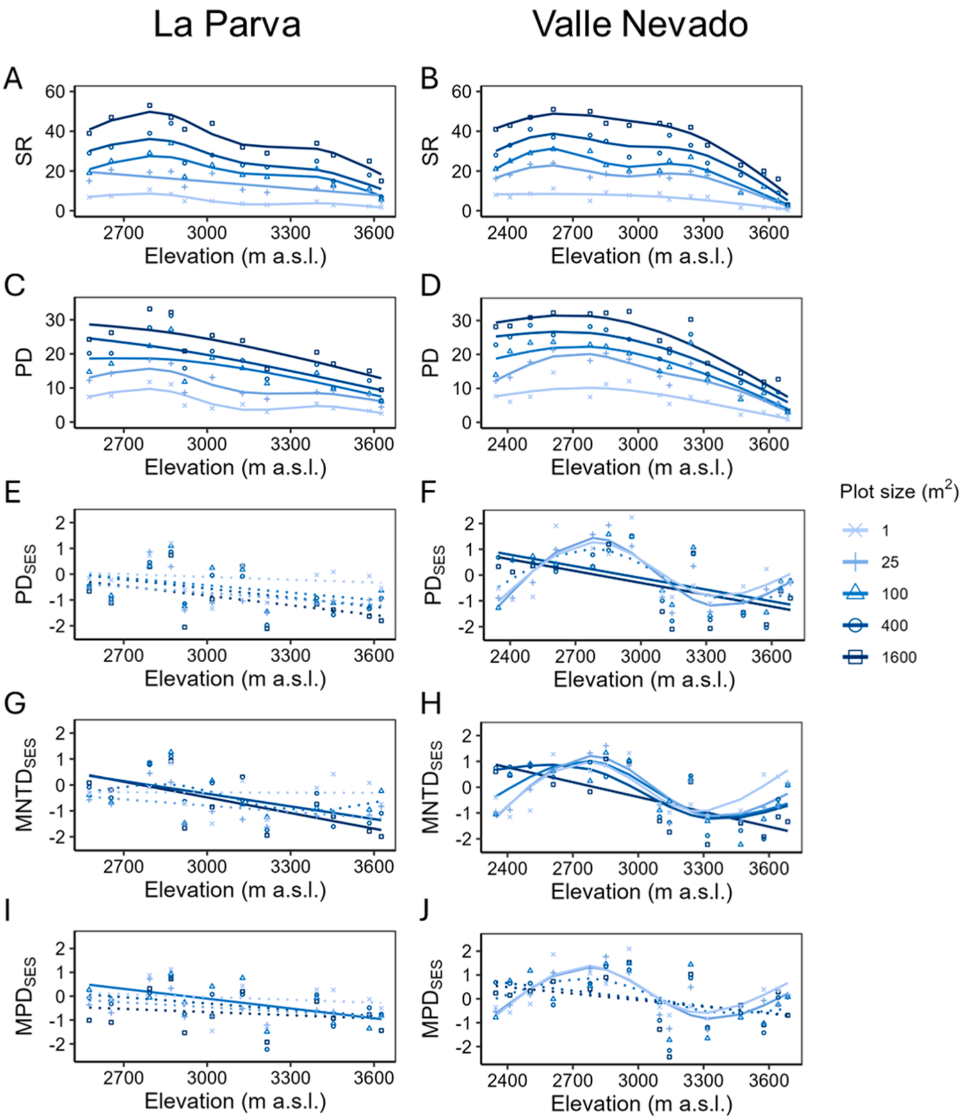

Fig. 3. Species richness (SR), Phylogenetic Diversity (PD), Standardized Effect Size of Phylogenetic Diversity (PD_{SES}), Standardized Effect Size of Mean Nearest Taxon Distance (MNTD_{SES}) and Standardized Effect Size of Mean Pairwise Distance (MPD_{SES}) in relation to elevation on the La Parva and Valle Nevado gradients. The analyses for the phylogenetic metrics were conducted using $\text{PHYLO}_{\text{sp.resolved}}$. A and B: SR; C and D: PD; E and F: PD_{SES}; G and H: MNTD_{SES}; I and J: MPD_{SES}. Solid lines indicate significant smooth terms of the GAM, while dotted lines indicate non-significance. Different symbols and line tones indicate different plot sizes. Lighter colours correspond to the smaller plots and darker colours to the larger plots. The curves correspond to the results of Generalized Additive Models. The points for 1 m^2 and 25 m^2 are the averages for the 5 replicates in each 1600 m^2 plot. Details for statistical tests are given in Table 1.

were performed using the ses.pd, ses.mpd and ses.mntd functions in the *picante* R-package (Kembel et al., 2010). All metrics were calculated for all plots sizes.

Preliminary exploration of the data revealed some nonlinear relationships between phylogenetic metrics and elevation of the plots. We therefore used generalized additive models (GAMs; Wood and Augustin, 2002). The cubic spline method was chosen as the smoothing function. GAMs were conducted using R package mgcv (Wood, 2017).

To determine the effect of phylogenetic resolution on the results, all phylogenetic metrics were recalculated for all plot sizes using $\mathrm{PHYLO}_{\mathrm{sp.polytomies.}}$ Given the non-normality of the data, Spearman correlation analysis was used to compare the individual site values of PD, $\mathrm{PD}_{\mathrm{SES}}$, $\mathrm{MPD}_{\mathrm{SES}}$ and $\mathrm{MNTD}_{\mathrm{SES}}$ obtained with the two phylogenies, respectively. Finally, to detect possible spatial scale effects, the values of the metrics obtained for each plot size using the two phylogenies were compared with the Wilcoxon signed-rank test for paired samples.

All analyses were performed in R version 4.1.2 (R Core Team, 2021).

3. Results

3.1. Species richness

We observed a gradual increase followed by a gradual decline in SR on both gradients. This local maximum roughly corresponded to the transition between the shrub-dominated subalpine belt and the true cushion-plant dominated alpine belt (Fig. 3. A, B). Thereafter SR decreased monotonically in the largest plots from 53 species (41.7 % of the total for the gradient) to 15 species (11.8 % of the total) in La Parva and from a maximum of 51 species (36.4 % of total species for the gradient) to a minimum of 3 species (2.1 % of total species) in Valle Nevado. Not surprisingly, SR decreased with diminishing plot size on both gradients (Fig. 3. A, B). Despite the overall drop in SR, on both gradients, many new species continued to appear for the first time up to as high as 3600 m a.s.l., indicating the continuous incorporation of new species over elevation (Fig. 4).

3.2. Phylogenetic diversity and phylogenetic structure

Notwithstanding a small dip at the lower elevations on the VN gradient, PD decreased with elevation at all spatial scales on both gradients (Fig. 3. C, D; Table 1). $\mathrm{PD}_{\mathrm{SES}}$ tended to decrease linearly with elevation, but only significantly on the Valle Nevado gradient and at the 400 m^2 and 1600 m^2 spatial scales where it transitioned from positive values (indicating more PD than expected in relation to species richness) below 3100 m to negative values thereafter (indicating less PD than expected). As spatial scale decreased, the relationship became non-linear (Fig. 3. E, F; Table 1).

$\mathrm{MNTD}_{\mathrm{SES}}$ significantly decreased linearly from positive to negative values with increasing elevation on both gradients at the largest spatial scale indicating a change from phylogenetic overdispersion on the lower parts of the gradients to phylogenetic clustering on the higher parts (Fig. 3. G, H; Table 1). On the La Parva gradient, a significant linear trend in the same direction was also found at the 400 m^2 spatial scale (Fig. 3 G). At all spatial scales smaller than 1600 m^2 on the Valle Nevado gradient, the relationship became non-linear and difficult to interpret in terms of elevational trends (Fig. 3. H).

For $\mathrm{MPD}_{\mathrm{SES}}$, the relationship with elevation was less clear (Table 1). On the La Parva gradient, $\mathrm{MPD}_{\mathrm{SES}}$ showed a significant linear tendency to decay with elevation, but only for the 100 m^2 plot (Fig. 3. I). In Valle Nevado, significant tendencies with elevation were detected only for the smaller 1 m^2 and 25 m^2 plots, but these followed a sinuous pattern without an evident elevational tendency (Fig. 3. J). In all other cases on both gradients, the relationship with elevation was non-significant.

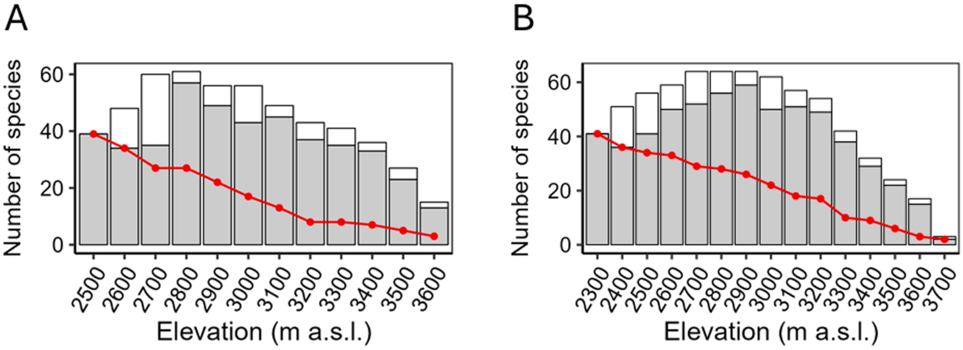

Fig. 4. Changes in species richness along the elevational gradient. The white bars indicate newly appearing species in each elevational band in relation to the previous band. The grey bars indicate species recorded in an elevational band that were carried over from the previous band. The red dots show the number of species recorded at the lowest elevation that continued to appear in successive elevational bands. When a species was missing between the highest and lowest band it was recorded for, it was added to the missing bands. A: La Parva; B: Valle Nevado.

Table 1
Results of generalized additive models showing the effect of elevation on SR and the four phylogenetic metrics for the five spatial scales sampled on the La Parva and Valle Nevado gradients. The analysis was conducted with PHYLO$_{sp.resolved}$. Models with significant smooth terms displaying a linear relationship are highlighted in bold. Other significant models that followed non-linear patterns in relationship to elevation are indicated with an asterisk (see Fig. 3 for details). SR: Species Richness; PD: Phylogenetic Diversity; PD$_{SES}$: Standardized Effect Size of Phylogenetic Diversity; MNTD$_{SES}$: Standardized Effect Size of Mean Nearest Taxon Distance; MPD$_{SES}$: Standardized Effect Size of Mean Pairwise Distance.

	La Parva									
Plot size (m^2)	SR		PD		PD$_{SES}$		MNTD$_{SES}$		MPD$_{SES}$	
	R^2	p-value	R^2	p-value	R^2	p-value	R^2	p-value	R^2	p-value
1	0.80	< 0.001 *	0.64	< 0.001 *	0.06	0.574	0.10	0.964	0.06	0.571
25	0.58	< 0.001 *	0.61	< 0.001 *	0.07	0.200	0.13	0.130	0.12	0.148
100	0.65	< 0.001 *	0.47	< 0.001 *	0.09	0.174	0.13	0.399	0.31	**0.036**
400	0.67	< 0.001 *	0.53	< 0.001 *	0.16	0.102	0.36	**0.023**	0.07	0.204
1600	0.87	< 0.001 *	0.62	< 0.001 *	0.14	0.130	0.40	**0.017**	0.05	0.543

	Valle Nevado									
Plot size (m^2)	SR		PD		PD$_{SES}$		MNTD$_{SES}$		MPD$_{SES}$	
	R^2	p-value	R^2	p-value	R^2	p-value	R^2	p-value	R^2	p-value
1	0.73	< 0.001 *	0.68	< 0.001 *	0.46	0.027 *	0.55	0.014 *	0.53	0.018 *
25	0.92	< 0.001 *	0.87	< 0.001 *	0.67	0.002 *	0.68	0.001 *	0.59	0.006 *
100	0.89	< 0.001 *	0.79	< 0.001 *	0.37	0.061 *	0.49	0.019 *	0.17	0.259
400	0.87	< 0.001 *	0.87	< 0.001 *	0.29	**0.023**	0.52	0.013 *	0.15	0.085
1600	0.95	< 0.001 *	0.87	< 0.001 *	0.27	**0.027**	0.52	**0.001**	0.83	0.157

3.3. *Effect of phylogenetic resolution*

PHYLO$_{sp.resolved}$ was well resolved at the tips as well as at deeper levels (Fig. S1). The presence of many genera in the study area represented by several species led to a significant number of polytomies in PHYLO$_{sp.polytomies}$ (Fig. S1). Overall, the results using the two phylogenies were significantly correlated at each spatial scale (Fig. 5). The main elevational trends did not change in direction (compare Table 1 with Table S3 and Fig. 3 with Fig. S2). However, comparison of individual site values separated according to plot size revealed a clear effect of sampling spatial scale. Specifically, the use of PHYLO$_{sp.polytomies}$ led to a significant decrease in PD across all spatial scales. In the case of PD$_{SES}$ and MNTD$_{SES,}$ significant differences accrued at the 100 m^2 and smaller spatial scales in the direction of more positive values (Table 2).

4. Discussion

The alpine zone, characterized by lack of trees and habitually cold temperatures, is the sole terrestrial biome that occurs at all latitudes across the globe (Körner, 2021). In that it can be easily replicated across many climatic zones and within regional floras, it

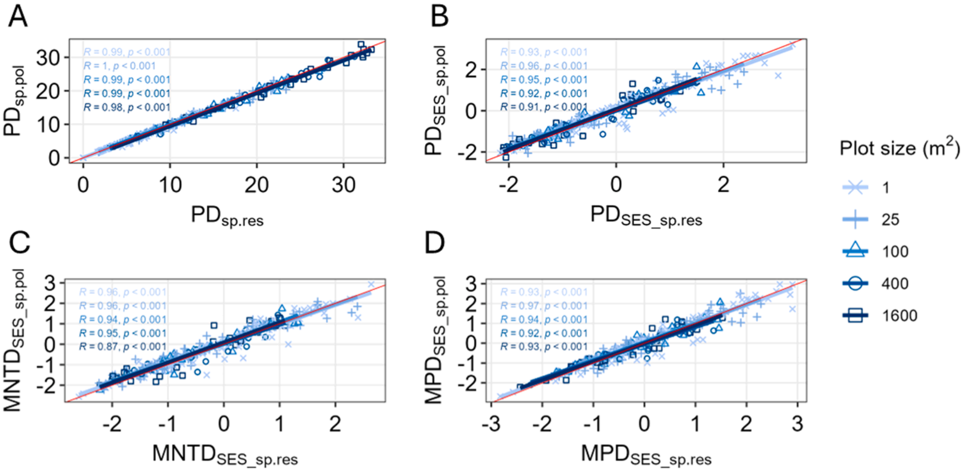

Fig. 5. Spearman correlation between four phylogenetic metric values calculated with PHYLO$_{sp.resolved}$ and PHYLO$_{sp.polytomies}$. Different symbols and line tones indicate different plot sizes. Lighter brighter colours correspond to the smaller plots and darker colours to larger plots. The data are for all elevations and plot sizes sampled on the two gradients. A: Phylogenetic Diversity (PD); B: Standardized Effect Size of Phylogenetic Diversity (PD$_{SES}$); C: Standardized Effect Size of Mean Nearest Taxon Distance (MNTD$_{SES}$); D:Standardized Effect Size of Mean Pairwise Distance (MPD$_{SES}$).

Table 2

Results of the Wilcoxon signed-rank test for paired samples comparing phylogenetic metrics calculated using PHYLO$_{\mathrm{sp.polytomies}}$ in relation to those calculated with PHYLO$_{\mathrm{sp.resolved}}$. Significant differences are highlighted in bold. The arrows indicate the predominant direction of change in the value of the metric. SR: Species Richness; PD: Phylogenetic Diversity; PD$_{\mathrm{SES}}$: Standardized Effect Size of Phylogenetic Diversity; MNTD$_{\mathrm{SES}}$: Standardized Effect Size of Mean Nearest Taxon Distance; MPD$_{\mathrm{SES}}$: Standardized Effect Size of Mean Pairwise Distance.

Plot size (m^2)	PD			PD$_{\mathrm{SES}}$			MNTD$_{\mathrm{SES}}$			MPD$_{\mathrm{SES}}$		
		V	p-value		V	p-value		V	p-value		V	p-value
1	⇓	265	**0.012**	⇑	113	**0.035**	⇑	127	**0.030**		101	0.114
25	⇓	273	**0.007**	⇑	64	**0.001**	⇑	74	**< 0.001**	⇑	44	**0.002**
100	⇓	263	**0.014**	⇑	119	**0.048**	⇑	138	**0.026**		108	0.115
400	⇓	302	**0.001**		152	0.193		184	0.105		136	0.458
1600	⇓	301	**0.001**		144	0.145		188	0.081		130	0.495

provides an exceptional opportunity to search for general patterns regarding phylogenetic structure along temperature gradients. We posited that if the TNC and OTT hypotheses for explaining the global latitudinal decline in biodiversity are meaningful in the terms of decreasing temperature with latitude, predictions arising from them should apply over elevational gradients —including between the tree line and the upper vegetation limit. Although these hypotheses have been examined by other workers over latitudinal and elevational gradients (e.g. Bañares-de-Dios et al., 2024; Li et al., 2022; Qian et al., 2018; Zhao et al., 2018), no previous study to the present work has explicitly examined them over elevation above tree line in the South American Andes.

Above tree line habitats comprise topographically induced mosaics of meso- and micro-climatic conditions (Scherrer and Körner, 2010) that can directly affect local species richness and taxonomic composition. Other factors, such as nutrient status and soil moisture have been shown to influence phylogenetic diversity and structure at local scales in the alpine habitat (López-Angulo et al., 2018a,b; Schroeder et al., 2024). These small-scale effects are likely to confound broad macroecological trends above tree line especially when a small scale is considered. Given the difficulty of controlling for exposition and micro-topographical variation in practice in high elevation gradient studies, we took the precaution of studying two separate gradients (within-study replication sensu Filazzola and Cahill, 2021) and included exceptionally large plots for alpine studies in our sampling scheme. We also asked a hitherto seemingly unresearched question. Does phylogenetic resolution affect the results obtained at different sampling spatial scales?

Based on the Generalized Additive Models, for MNTD$_{\mathrm{SES}}$ we found evidence for phylogenetic overdispersion at subalpine elevations transitioning to phylogenetic clustering in the upper alpine belt but only at the largest or two larger spatial scales sampled. That this tendency was observed over two separate above tree line gradients that share a regional flora lends strong support to the TNC hypothesis. PD$_{\mathrm{SES}}$ decreased with elevation on the Valle Nevado gradient which again is consistent with predictions of the TNC hypothesis. Interesting, while overall species richness declined with elevation, new species continued to appear, even at the highest reaches. This result is also congruous with the TNC hypothesis where recent speciation is expected within lineages throughout the alpine. Knowledge of divergence times over the alpine gradient is desirable to shed more light on this possibility. Other tightly sampled studies that have concentrated on or include above tree line communities have reported phylogenetic clustering as the norm above tree line (Zhang et al., 2020) or show a trend towards increased phylogenetic clustering as elevation increases (Li et al., 2014; Manish and Pandit, 2018). All these results support the TNC hypothesis, as they indicate phylogenetic clustering is prevalent above the tree line and tends to increase with elevation. However, in at least one study, following a zig-zag pattern, the trend was for increasing phylogenetic overdispersion over elevation within the alpine (Li et al., 2022). In this case, the authors argued both OTT and TNC hypotheses explained phylogenetic structure at low and middle elevations respectively, but in this case of the alpine zone, effect of facilitation between distantly related species was invoked. In a similar way, very high screes in the Hengduan mountains also showed phylogenetic overdispersion (Li et al., 2014), but they were subtended by a clear pattern of increasing phylogenetic clustering, as expected under TNC.

Although the elevational trend in phylogenetic structure seen in our study area conforms well to the TNC hypothesis, there are certain nuances. Phylogenetic overdispersion in the subalpine belt was unexpected and is worth elaborating on. Biogeographically, the tree line can be conceived as a "hard barrier" that imposes a stringent filter on lineages colonizing into above tree line habitats. Under this scenario, significant phylogenetic clustering, although not as strong as found in the upper alpine, might have been expected in the subalpine belt. One possible explanation for phylogenetic overdispersion in the subalpine belt resides in the appearance of the mediterranean-type climate in central Chile that appeared as of the Miocene coeval with the uplift of the Andes and its effects on the tree line.

Globally, tree line ecotones vary from abrupt tree lines to extended zones of increasingly small, stunted and/or dispersed trees (Bader et al., 2021). The *K. angustifolia* tree line conforms to the small and dispersed tree type. Moreover, this tree line is depressed in elevation (attributable to aridity) in relation to the typically temperature-defined tree line (Piper et al., 2016). The *Kageneckia* tree line lies at around 2200–2300 m. Based on the lapse rate of $-5.9\,^{\circ}\mathrm{C}\ \mathrm{km}^{-1}$ provided here, MAT at 2200 m would be 10.2 °C which is considerably higher than estimated MAT reported for a large number of temperate tree lines in a northern and a southern hemisphere country (4.5–7.8 °C and 4.6–7.3 °C, respectively; Rita et al., 2023). That introduced watered ornamental northern hemisphere trees can grow on roadsides to around 2700–2800 m in our study area supports the hypothesis that the "climatic tree line" sensu (Körner, 2007) is higher than the natural *K. angustifolia* tree line. Under this scenario, the present-day shrubby subalpine belt is likely to have congealed out of upper montane woodland after the tree line began to descend in elevation as of the Miocene with the inception of the summer drought (Rundel et al., 2016). Support for the above explanation is seen in the presence of many subalpine species in open spaces in *Kageneckia* woodland. As the Andes began to uplift in the Miocene, summer temperatures would have increased, compensating for the reduction in growing season temperature due to uplift. Effectively subalpine vegetation would have been carried up with uplift but would not have experienced a large temperature change over the growing season. As evidenced by the gradual increase followed by a gradual decline in species richness in the transition between the subalpine and "true" alpine belt, the onset of summer drought in the Miocene seems also to have affected species richness in the subalpine belt. The above interpretation stresses that the changes in seasonality leading to warmer and drier summers superimposed over a general decrease in temperature due to mountain building can lead to unexpected phylogenetic structure. Indeed, it would not be surprising if this Mediterranean-climate effect were to be seen at mid latitudes over the latitudinal gradient. A relevant question, here, is whether subalpine vegetation would have continued to show overdispersion if additional vegetation belts found below the tree line had been included in our study. In any case, even if the subalpine became clustered, this would not affect the overall tendency towards greater clustering at the highest elevations, as the later probably would increase.

An important result emerging from our study is that $MNTD_{SES}$ but not MPD_{SES} showed a clear tendency to decline with elevation. $MNTD_{SES}$ mainly reflects structure in the shallower parts of a phylogeny while MPD_{SES} is more sensitive to detecting structure in its deeper parts (Webb, 2000). The above combination of results could be interpreted as evidence of recent radiation in terminal clusters in the upper alpine (where significant clustering was found) that has been preceded by a limited amount of deep level phylogenetic filtering in the early stages of development of above tree line vegetation. Perhaps, at higher elevations in the central Chilean Andes, filtering for non-conserved traits such as the capacity to form cushions has played a greater role in early community assembly than filtering for conserved traits. In support of the last argument, cushion species in the upper alpine in our study area belong to many genera and plant families (e.g., *Oxalis*, *Azorella*, *Nototriche*, *Anarthrophyllum*, *Junellia*). Most of these genera have large numbers of species in the upper alpine. Cushion forms are known to have evolved on at least 115 occasions spread across the Angiosperm phylogenetic tree (Boucher et al., 2016). The implication here is that functional traits can override niche conservatism when selective pressures are very strong. To test the above ideas more information on strongly conserved versus non-conserved traits is needed.

To date, many studies focusing on specific elevational or temperature gradients have compared phylogenetic structure based on data obtained in plots of a fixed size which vary in size according to study (e.g., Luo et al., 2023; Qian et al., 2014; but see Zhang et al., 2020, for an exception) or in equal-sized transects (Schroeder et al., 2024). Overall, our largest plots showed a tendency for a linear relationship between $MNTD_{SES}$ and elevation. As the plots became smaller the relationship tended to become sinuous indicating that meso- and micro-scale ecological effects were coming into play. Some authors, working at large spatial scales, have interpreted sinuous curves as evidence of an alternation of the expectations of the TNC and OTT hypotheses (e.g., Li et al., 2022). However, in our case, ecological effects are more likely explanation. For example, for $MNTD_{SES}$, a sharp peak of phylogenetic overdispersion occurred at mid-low elevations and a sharp peak of phylogenetic clustering in the very high plots was observed in plot sizes up to the 400 m^2 spatial scale in the Valle Nevado gradient. The first peak corresponded roughly to where species richness reached a maximum on that gradient and cover is high, while the second corresponded to where species richness was very low and the vegetation more dispersed. At relatively small spatial grains, co-occurring species tend to be more distantly related due to competition (Duarte et al., 2021; Kraft and Ackerly, 2010) which would tend to increase phylogenetic overdispersion when species richness and cover are high. On the contrary, when richness and vegetation cover are low, competition would play a lesser role in determining the composition of species assemblages, thereby allowing more closely related species to coexist. These caveats underscore that large sampling units are essential to overcome local ecological effects when looking for macroecological patterns across above tree line gradients. For example, using data obtained in 7–8 replicated 10 m line transects in the same general area as this study, Schroeder et al. (2024) found much variation in NRI across the elevational gradient which was difficult to interpret. Our results show that 1600 m^2 plots were optimal to avoid confounding ecological effects in our system. This result contrasts to the findings of Zhang et al. (2020) on the Tibetan Plateau who found similar results at the 3 m^2 and 1000 m^2 spatial scales. The difference is likely to be due to low plant cover yet very high diversity in the central Chilean Andes. The effect of plot size detected here is also likely to be relevant in studies of forests along elevational gradients, especially in tropical latitudes where species richness is very high at lower elevations. Several studies have looked at phylogenetic diversity and/or phylogenetic structure over elevational and the latitudinal gradients based on interpolation of species presences between the recorded extremes of elevational ranges of species (e.g. Di Musciano et al., 2024; Li et al., 2014; Manish, 2021). This method has the advantage of producing aesthetically smoother curves. However, it is likely to over-represent the presence of certain species. Species exclusion on a gradient is not necessarily a product of inadequate sampling by botanists. It can also arise naturally through limiting similarity (Meszéna et al., 2006), a relevant phenomenon in the community assembly process. Species abundance data would be useful to approach ecological concerns like competition and exclusions. Abundance was not measured in this study as maximum lineage coverage was prioritized. The latter is harder to achieve when species' presences are extracted from sampling for abundance. Common methods to measure abundance in ecological studies (e.g. line transects, point sampling methods) have a high probability of missing rare species (Goslee, 2006), which will affect phylogenetic structure.

In this study, nested plots were used to account for scale effects on elevational trends in phylogenetic diversity and structure. While nested plots have the drawback of not being entirely statistically independent of one another, finding homogeneous areas of vegetation for the placement of large numbers of independent plots in the alpine environment is challenging. The use of nested plots to assess plot size effect ensures that environmental conditions for all plot sizes at a given elevation are as similar as possible in a highly heterogeneous environment. This sampling scheme, combined with sampling over two independent gradients where environmental conditions (e.g., soil properties, substrate type, site exposition) will not necessarily be the same, provides a parsimonious sampling strategy for detecting broad scale elevational patterns.

Finally, many current studies focusing on phylogenetic structure over latitudinal and altitudinal gradients rely on megaphylogenies generated by programs such as Phylomatic (Webb and Donoghue, 2005) and V.PhyloMaker (Jin and Qian, 2019) (e.g. Di Musciano et al., 2024; Duarte et al., 2021; Lapiedra et al., 2015; Li et al., 2014) which although reasonably resolved at the generic level, are less so at the species level. Alternatively, to obtain a species-level phylogeny, species are added manually to a generic-level phylogeny as polytomies (cf. Chalmandrier et al., 2015). It could be argued that accurate detection of phylogenetic structure in youthful alpine systems such as in the South American Andes, where many recent speciation events are to be expected, requires well resolved phylogenies at the species level. In accordance with Qian and Jin (2021), using a well resolved species-level phylogeny and a phylogeny where species of a genus were represented by equal branches, values of all phylogenetic metrics we employed were closely correlated. Nevertheless, closer examination revealed site differences in the direction of less PD at all spatial scales and increases for PD_{SES} and $MNTD_{SES}$ for the 100 m^2 and smaller sized plots. These differences were not detected at the two largest spatial scales when the poorly resolved species-level phylogeny was used. Increased $MNTD_{SES}$ in the smaller sized plots signifies a trend toward less clustering in a relative sense. If, for example, we had focused on temperature variation due to microtopography and soil types as drivers of phylogenetic structure, such differences would have been relevant. The take home message is that while well resolved phylogenies are important for ecological interpretations (cf. López-Angulo et al., 2018a,b for good examples) they become less important for detecting general elevational trends always that very large plots are sampled. Given these considerations, we feel confident that the phylogenetic clustering detected in the upper parts of the alpine in the central Chilean Andes revealed through the analysis of our largest plots is a reliable macroecological result.

5. Conclusions

Our findings suggest that the TNC hypothesis lends itself to the assembly of plant communities in above tree line communities in the central Chilean Andes. We found no evidence to support the OTT hypothesis. We stress that aside from using large plots to overcome micro-topographical and ecological effects on species richness and composition on above tree line gradients, searching for generalities on more than one gradient sharing a regional flora is useful, given the difficulties of controlling for exposition and other meso-scale ecological effects such as soil type in steep, dissected mountainous terrain. Well resolved phylogenies are recommended in ecological studies when very small spatial scales are considered. The level of resolution of the phylogeny becomes less important as the size of the sampling units increases.

Interestingly, Qian et al. (2021), in their comparison of alpine and regional floras, found that phylogenetic clustering in tropical alpine floras exceeds that in their temperate counterparts. In the South American Andes, this trend is not unexpected given the large species swarms in genera such as *Lupinus*, *Gentianella*, *Valeriana*, *Hypericum* in the northern part of the range (Arroyo and Cavieres, 2013; Madriñán et al., 2013; Sklenář et al., 2011). Alternatively, the latitudinal difference could be due to phylogenetic clustering appearing only at very high elevations in the temperate zone (as we found here) and thus being less pronounced in the total alpine flora. Detailed gradient studies at other latitudes along the 68 degrees of latitude traversed by the climatically diverse South American Andes are necessary to untangle these possibilities.

Ethical statement

This research did not involve any studies with human participants, animals, or sensitive data. No ethical approval was required.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

This work was supported by FONDECYT Grant 1221540 (M.T.K.A., P.J-A., and I.T.). Additional support was provided by ANID PIA/BASAL Grant PFB210018 to the International Cape Horn Center (CHIC) and ANID PIA/BASAL Grant FB210006 to the Institute of Ecology and Biodiversity (IEB) (I.T., M.T.K.A., and P.J-A.), as well as ANID Doctoral Fellowship 21200714 (I.T.) and FONDECYT Grant 1230717 (P.J-A.). We thank Valeria Robles, Karina Robles, Jonas Arenas, Luis Retamal, and Muriel Acevedo for their assistance with plot sampling and Valeria Robles for providing the image of *Viola atropurpurea*.

Data availability

https://doi.org/10.17632/jd25sfgxv4.1

References

Arroyo, M.T.K., Cavieres, L.A., 2013. High-elevation andean ecosystems. Encyclopedia of Biodiversity. Elsevier, pp. 96–110. https://doi.org/10.1016/B978-0-12-384719-5.00428-7.

Arroyo, M.T.K., Tamburrino, Í ., Robles, V., Robles, K., Loreto, V., M, 2024. Data on vascular plant species composition along two elevation gradients in the high Andes of central Chile (33°S). Data Brief.

Bader, M.Y., Llambí, L.D., Case, B.S., Buckley, H.L., Toivonen, J.M., Camarero, J.J., Cairns, D.M., Brown, C.D., Wiegand, T., Resler, L.M., 2021. A global framework for linking alpine-treeline ecotone patterns to underlying processes. Ecography 44, 265–292. https://doi.org/10.1111/ecog.05285.

Bañares-de-Dios, G., Macía, M.J., Arellano, G., Granzow-de la Cerda, Í ., Vega-Álvarez, J., Arnelas, I., Espinosa, C.I., Salinas, N., Cayuela, L., 2024. Woody plant taxonomic, functional, and phylogenetic diversity decrease along elevational gradients in Andean tropical montane forests: environmental filtering and arrival of temperate taxa. Plant Divers 46, 491–501. https://doi.org/10.1016/j.pld.2024.03.005.

Bell, C.D., Kutschker, A., Arroyo, M.T.K., 2012. Phylogeny and diversification of valerianaceae (Dipsacales) in the southern Andes. Mol. Phylogenet Evol. 63, 724–737. https://doi.org/10.1016/J.YMPEV.2012.02.015.

Boucher, F.C., Lavergne, S., Basile, M., Choler, P., Aubert, S., 2016. Evolution and biogeography of the cushion life form in angiosperms. Perspect. Plant Ecol. Evol. Syst. 20, 22–31. https://doi.org/10.1016/j.ppees.2016.03.002.

Cavieres, L.A., Badano, E.I., Sierra-Almeida, A., Gómez-González, S., Molina-Montenegro, M.A., 2006. Positive interactions between alpine plant species and the nurse cushion plant Laretia acaulis do not increase with elevation in the Andes of central Chile. N. Phytol. 169, 59–69. https://doi.org/10.1111/j.1469-8137.2005.01573.x.

Cavieres, L.A., Peñaloza, A., Kalin Arroyo, M., 2000. Altitudinal vegetation belts in the high-Andes of central Chile (33°S). Rev. Chil. De. Hist. Nat. 73. https://doi.org/10.4067/S0716-078X2000000200008.

Chalmandrier, L., Münkemüller, T., Lavergne, S., Thuiller, W., 2015. Effects of species' similarity and dominance on the functional and phylogenetic structure of a plant meta-community. Ecology 96, 143–153. https://doi.org/10.1890/13-2153.1.

Crisp, M.D., Arroyo, M.T.K., Cook, L.G., Gandolfo, M.A., Jordan, G.J., McGlone, M.S., Weston, P.H., Westoby, M., Wilf, P., Linder, H.P., 2009. Phylogenetic biome conservatism on a global scale. Nature 2009 458 (7239), 754–756. https://doi.org/10.1038/nature07764.

Cuesta, F., Carilla, J., LLambí, L.D., Muriel, P., Lencinas, M.V., Meneses, R.I., Feeley, K.J., Pauli, H., Aguirre, N., Beck, S., Bernardi, A., Cuello, S., Duchicela, S.A., Eguiguren, P., Gamez, L.E., Halloy, S., Hudson, L., Jaramillo, R., Peri, P.L., Ramírez, L.A., Rosero-Añazco, P., Thompson, N., Yager, K., Tovar, C., 2023. Compositional shifts of alpine plant communities across the high Andes. Glob. Ecol. Biogeogr. 32, 1591–1606. https://doi.org/10.1111/GEB.13721.

Di Castri, F., Hajek, E.R., 1976. Bioclimatología de Chile. Editorial Universidad Católica de Chile, Santiago.

Di Musciano, M., Calvia, G., Ruggero, A., Farris, E., Ricci, L., Frattaroli, A.R., Bagella, S., 2024. Elevational patterns of plant species richness and phylogenetic diversity in a Mediterranean island. Perspect. Plant Ecol. Evol. Syst. 65, 125815. https://doi.org/10.1016/J.PPEES.2024.125815.

Duarte, M., Verdú, M., Cavieres, L.A., Bustamante, R.O., 2021. Plant–plant facilitation increases with reduced phylogenetic relatedness along an elevation gradient. Oikos 130, 248–259. https://doi.org/10.1111/oik.07680.

Faith, D.P., 1992. Conservation evaluation and phylogenetic diversity. Biol. Conserv 61, 1–10. https://doi.org/10.1016/0006-3207(92)91201-3.

Filazzola, A., Cahill, J.F., 2021. Replication in field ecology: identifying challenges and proposing solutions. Methods Ecol. Evol. 12, 1780–1792. https://doi.org/10.1111/2041-210X.13657.

Gagnon, E., Ringelberg, J.J., Bruneau, A., Lewis, G.P., Hughes, C.E., 2019. Global succulent biome phylogenetic conservatism across the pantropical caesalpinia group (Leguminosae). N. Phytol. 222, 1994–2008. https://doi.org/10.1111/nph.15633.

Gaston, K.J., 2000. Global patterns in biodiversity. Nature 405, 220–227. https://doi.org/10.1038/35012228.

Goslee, S.C., 2006. Behavior of vegetation sampling methods in the presence of spatial autocorrelation. Plant Ecol. 187, 203–212. https://doi.org/10.1007/s11258-005-3495-x.

Guo, Q., Kelt, D.A., Sun, Z., Liu, H., Hu, L., Ren, H., Wen, J., 2013. Global variation in elevational diversity patterns. Sci. Rep. 2013 3 (1), 1–7. https://doi.org/10.1038/srep03007.

Hillebrand, H., 2004. On the generality of the latitudinal diversity gradient. Am. Nat. 163, 192–211. https://doi.org/10.1086/381004.

Jablonski, D., Roy, K., Valentine, J.W., 2006. Out of the tropics: evolutionary dynamics of the latitudinal diversity gradient. Science 314 (1979), 102–106. https://doi.org/10.1126/science.1130880.

Jin, Y., Qian, H., 2019. V.PhyloMaker: an R package that can generate very large phylogenies for vascular plants. Ecography 42, 1353–1359. https://doi.org/10.1111/ecog.04434.

Kembel, S.W., Cowan, P.D., Helmus, M.R., Cornwell, W.K., Morlon, H., Ackerly, D.D., Blomberg, S.P., Webb, C.O., 2010. Picante: R tools for integrating phylogenies and ecology. Bioinformatics 26, 1463–1464. https://doi.org/10.1093/bioinformatics/btq166.

Körner, C., 2007. Climatic treelines: conventions, global patterns, causes. Erdkunde 61, 316–324. https://doi.org/10.3112/erdkunde.2007.04.02.

Körner, C., 2021. Alpine Plant Life, Alpine Plant Life. Springer International Publishing. https://doi.org/10.1007/978-3-030-59538-8.

Kraft, N.J.B., Ackerly, D.D., 2010. Functional trait and phylogenetic tests of community assembly across spatial scales in an Amazonian forest. Ecol. Monogr. 80, 401–422. https://doi.org/10.1890/09-1672.1.

Lapiedra, O., Sol, D., Traveset, A., Vilà, M., 2015. Random processes and phylogenetic loss caused by plant invasions. Glob. Ecol. Biogeogr. 24, 774–785. https://doi.org/10.1111/geb.12310.

Li, L., Xu, X., Qian, H., Huang, X., Liu, P., Landis, J.B., Fu, Q., Sun, L., Wang, H., Sun, H., Deng, T., 2022. Elevational patterns of phylogenetic structure of angiosperms in a biodiversity hotspot in eastern Himalaya. Divers Distrib. 28, 2534–2548. https://doi.org/10.1111/ddi.13513.

Li, X., Zhu, X., Niu, Y., Sun, H., 2014. Phylogenetic clustering and overdispersion for alpine plants along elevational gradient in the Hengduan Mountains Region, southwest China. J. Syst. Evol. 52, 280–288. https://doi.org/10.1111/jse.12027.

López-Angulo, J., Pescador, D.S., Sánchez, A.M., Mihoč, M.A.K., Cavieres, L.A., Escudero, A., 2018. Determinants of high mountain plant diversity in the Chilean Andes: from regional to local spatial scales. PLoS One 13, e0200216. https://doi.org/10.1371/journal.pone.0200216.

López-Angulo, J., Swenson, N.G., Cavieres, L.A., Escudero, A., 2018. Interactions between abiotic gradients determine functional and phylogenetic diversity patterns in Mediterranean-type climate mountains in the Andes. J. Veg. Sci. 29, 245–254. https://doi.org/10.1111/jvs.12607.

Luo, Y., Zhou, M., Jin, S., Wang, Q., Yan, D., 2023. Changes in phylogenetic structure and species composition of woody plant communities across an elevational gradient in the southern Taihang Mountains, China. Glob. Ecol. Conserv 42, e02412. https://doi.org/10.1016/j.gecco.2023.e02412.

Madriñán, S., Cortés, A.J., Richardson, J.E., 2013. Páramo is the world's fastest evolving and coolest biodiversity hotspot. Front. Genet. 4. https://doi.org/10.3389/fgene.2013.00192.

Manish, K., 2021. Species richness, phylogenetic diversity and phylogenetic structure patterns of exotic and native plants along an elevational gradient in the Himalaya. Ecol. Process 10, 1–13. https://doi.org/10.1186/s13717-021-00335-z.

Manish, K., Pandit, M.K., 2018. Phylogenetic diversity, structure and diversification patterns of endemic plants along the elevational gradient in the Eastern Himalaya. Plant Ecol. Divers 11, 501–513. https://doi.org/10.1080/17550874.2018.1534147.

Meszéna, G., Gyllenberg, M., Pásztor, L., Metz, J.A.J., 2006. Competitive exclusion and limiting similarity: a unified theory. Theor. Popul Biol. 69, 68–87. https://doi.org/10.1016/J.TPB.2005.07.001.

Pérez, F., Lavandero, N., Ossa, C.G., Hinojosa, L.F., Jara-Arancio, P., Arroyo, M.T.K., 2020. Divergence in plant traits and increased modularity underlie repeated transitions between low and high elevations in the andean genus leucheria. Front. Plant Sci. 11. https://doi.org/10.3389/fpls.2020.00714.

Peterson, A.T., Soberón, J., Sánchez-Cordero, V., 1999. Conservatism of ecological niches in evolutionary time. Science 285 (1979), 1265–1267. https://doi.org/10.1126/science.285.5431.1265.

Piper, F.I., Viñegla, B., Linares, J.C., Camarero, J.J., Cavieres, L.A., Fajardo, A., 2016. Mediterranean and temperate treelines are controlled by different environmental drivers. J. Ecol. 104, 691–702. https://doi.org/10.1111/1365-2745.12555.

Qian, H., Hao, Z., Zhang, J., 2014. Phylogenetic structure and phylogenetic diversity of angiosperm assemblages in forests along an elevational gradient in Changbaishan, China. J. Plant Ecol. 7, 154–165. https://doi.org/10.1093/jpe/rtt072.

Qian, H., Jin, Y., 2021. Are phylogenies resolved at the genus level appropriate for studies on phylogenetic structure of species assemblages? Plant Divers 43, 255–263. https://doi.org/10.1016/j.pld.2020.11.005.

Qian, H., Ricklefs, R.E., 2016. Out of the tropical lowlands: latitude versus elevation. Trends Ecol. Evol. 31, 738–741. https://doi.org/10.1016/j.tree.2016.07.012.

Qian, H., Ricklefs, R.E., Thuiller, W., 2021. Evolutionary assembly of flowering plants into sky islands. Nat. Ecol. Evol. 5, 640–646. https://doi.org/10.1038/s41559-021-01423-1.

Qian, H., Zhang, J., Hawkins, B.A., 2018. Mean family age of angiosperm tree communities and its climatic correlates along elevational and latitudinal gradients in eastern North America. J. Biogeogr. 45, 259–268. https://doi.org/10.1111/jbi.13108.

R Core Team, 2021. R: A language and environment for statistical computing.

Rambaut, A., Suchard, M., Xie, D., Drummond, A., 2014. Tracer.

Rita, A., Saracino, A., Cieraad, E., Saulino, L., Zotti, M., Idbella, M., De Stefano, C., Mogavero, V., Allevato, E., Bonanomi, G., 2023. Topoclimate effect on treeline elevation depends on the regional framework: A contrast between Southern Alps (New Zealand) and Apennines (Italy) forests. Ecol. Evol. 13. https://doi.org/10.1002/ece3.9733.

Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D.L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A., Huelsenbeck, J.P., 2012. MrBayes 3.2: efficient bayesian phylogenetic inference and model choice across a large model space. Syst. Biol. 61, 539–542. https://doi.org/10.1093/sysbio/sys029.

Rundel, P.W., Arroyo, M.T.K., Cowling, R.M., Keeley, J.E., Lamont, B.B., Vargas, P., 2016. Mediterranean biomes: evolution of their vegetation, floras, and climate. Annu Rev. Ecol. Evol. Syst. 47, 383–407. https://doi.org/10.1146/annurev-ecolsys-121415-032330.

Scherrer, D., Körner, C., 2010. Infra-red thermometry of alpine landscapes challenges climatic warming projections. Glob. Chang Biol. 16, 2602–2613. https://doi.org/10.1111/j.1365-2486.2009.02122.x.

Scherson, R.A., Vidal, R., Sanderson, M.J., 2008. Phylogeny, biogeography, and rates of diversification of New World Astragalus (Leguminosae) with an emphasis on South American radiations. Am. J. Bot. 95, 1030–1039. https://doi.org/10.3732/AJB.0800017.

Schroeder, L., Robles, V., Jara-Arancio, P., Lapadat, C., Hobbie, S.E., Arroyo, M.T.K., Cavender-Bares, J., 2024. Drivers of plant diversity, community composition, functional traits, and soil processes along an alpine gradient in the central Chilean Andes. Ecol. Evol. 14. https://doi.org/10.1002/ece3.10888.

Shaheen, H., Aziz, S., Nasar, S., Waheed, M., Manzoor, M., Siddiqui, M.H., Alamri, S., Haq, S.M., Bussmann, R.W., 2023. Distribution patterns of alpine flora for long-term monitoring of global change along a wide elevational gradient in the Western Himalayas. Glob. Ecol. Conserv 48, e02702. https://doi.org/10.1016/j.gecco.2023.e02702.

Sklenář, P., Dušková, E., Balslev, H., 2011. Tropical and temperate: evolutionary history of páramo flora. Bot. Rev. 77, 71–108. https://doi.org/10.1007/s12229-010-9061-9.

Webb, C.O., 2000. Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. Am. Nat. 156, 145–155. https://doi.org/10.1086/303378.

Webb, C., Donoghue, M.J., 2005. Phylomatic: tree assembly for applied phylogenetics. Mol. Ecol. Notes 5, 181–183. https://doi.org/10.1111/j.1471-8286.2004.00829.x.

Wiens, J.J., Ackerly, D.D., Allen, A.P., Anacker, B.L., Buckley, L.B., Cornell, H.V., Damschen, E.I., Jonathan Davies, T., Grytnes, J.A., Harrison, S.P., Hawkins, B.A., Holt, R.D., McCain, C.M., Stephens, P.R., 2010. Niche conservatism as an emerging principle in ecology and conservation biology. Ecol. Lett. 13, 1310–1324. https://doi.org/10.1111/J.1461-0248.2010.01515.X.

Wiens, J.J., Donoghue, M.J., 2004. Historical biogeography, ecology and species richness. Trends Ecol. Evol. 19, 639–644. https://doi.org/10.1016/j.tree.2004.09.011.

Wood, S.N., 2017. Generalized additive models: An introduction with R, second edition. Generalized Additive Models: An Introduction with R, Second Edition 1–476. https://doi.org/10.1201/9781315370279.

Wood, S.N., Augustin, N.H., 2002. GAMs with integrated model selection using penalized regression splines and applications to environmental modelling. Ecol. Model. 157, 157–177. https://doi.org/10.1016/S0304-3800(02)00193-X.

Zhang, C., Zhou, H., Ma, Z., 2020. Phylogenetic structure of alpine steppe plant communities along a precipitation and temperature gradient on the Tibetan Plateau. Glob. Ecol. Conserv 24, e01379. https://doi.org/10.1016/j.gecco.2020.e01379.

Zhao, M., Wang, Y., Xue, F., Zuo, W., Xing, K., Wang, G., Kang, M., Jiang, Y., 2018. Elevational patterns and ecological determinants of mean family age of angiosperm assemblages in temperate forests within Mount Taibai, China. J. Plant Ecol. 11, 919–927. https://doi.org/10.1093/jpe/rty001.