Received: 17 September 2024 | Accepted: 12 May 2025

DOI: 10.1111/1365-2745.70089

Journal of Ecology

RESEARCH ARTICLE

Functional and phylogenetic similarity between native and non-native plant species along an elevational gradient in the central Chilean Andes: No evidence for the preadaptation hypothesis

Vinka Anic[1,2] | Maritza Mihoč[1,2] | Graciela Valencia[1,2] | Claudia Reyes-Bahamonde[1,2,3] | León A. Bravo[4] | Patricia L. Sáez[2,4] | Aníbal Pauchard[2,5] | Lohengrin A. Cavieres[1,2]

[1]Departamento de Botánica, Facultad de Ciencias Naturales y Oceanográficas, Universidad de Concepción, Concepción, Chile

[2]Instituto de Ecología y Biodiversidad (IEB), Santiago, Chile

[3]Millenium Nucleus of Patagonian Limit of Life (LiLi), Valdivia, Chile

[4]Departamento de Ciencias Agronómicas y Recursos Naturales, Facultad de Ciencias Agropecuarias y Medioambiente, Universidad de La Frontera, Temuco, Chile

[5]Laboratorio de Invasiones Biológicas (LIB), Facultad de Ciencias Forestales, Universidad de Concepción, Concepción, Chile

Correspondence
Vinka Anic
Email: vinkanict@hotmail.com

Lohengrin A. Cavieres
Email: lcaviere@udec.cl

Funding information
Chilean National Agency for Research and Development (ANID), Grant/Award Number: ACT210038, FB210006, FONDECYT 1211197 and FONDECYT 1211231

Handling Editor: Kimberley Simpson

Abstract

1. The preadaptation hypothesis proposed by Darwin states that non-native species phylogenetically close to natives may be successful in the introduced area, as closely related species may exhibit similar adaptations to the environment. In support of this hypothesis, both resident and non-native plant species have been described as sharing conservative functional traits when subject to habitat filtering, including low leaf area and specific leaf area (SLA). The central Chilean Andes, influenced by a Mediterranean-type climate, show opposite elevational gradients of water availability and temperature. In this mountain region, low-elevation drought and high-elevation cold temperatures may promote a conservative growth strategy in coexisting native and non-native plant species, thereby reducing the phylogenetic and functional distances between these two species groups. Here, we tested this hypothesis by studying the phylogenetic and functional similarity between co-occurring native and non-native plant species along a wide elevational gradient.
2. We measured six leaf functional traits in native ($N=91$) and non-native ($N=26$) plant species from roadside habitats at six elevations (from 1200 to 3600 m a.s.l.) in the central Chilean Andes. The traits comprised leaf area, SLA, leaf dry matter content, leaf thickness, and leaf nitrogen and chlorophyll contents. The mean functional and phylogenetic distances of focal non-native species relative to the native species in the community were calculated.
3. Contrary to our predictions, we found no significant effect of elevation on the functional and phylogenetic distances between native and non-native plant species.
4. Native species showed reduced SLA in habitats under drought conditions and smaller leaves above the tree line. In contrast, non-native species exhibited high

leaf area values along the entire elevational gradient and high SLA in habitats affected by summer drought.

5. *Synthesis*. Our study provides novel evidence of the phylogenetic relatedness and functional differentiation between native and non-native plant species in habitats influenced by summer drought or low-temperature stress in the central Chilean Andes. In these harsh environments, the acquisitive leaf traits found in non-native species suggest that the growth strategy of these species could be affected by disturbance and/or the modification of the environment by nurse plants.

KEYWORDS

alpine plants, central Chilean Andes, elevational gradient, leaf functional traits, non-native species, phylogenetic similarity, summer drought

1 | INTRODUCTION

One of the major goals for invasion ecology is to reveal the factors underpinning the success of non-native species in the introduced range (Le Roux, 2021; Richardson, 2011). Invasion success of non-native plants could be affected by a myriad of factors such as environmental filters, propagule pressure and the properties of the recipient community, including native species richness and the presence of natural enemies (Gioria et al., 2023; Naeem et al., 2000). Intrinsic factors, including an elevated fecundity (Richardson & Rejmánek, 2004) and the capacity to change plant functional traits (i.e. morpho-physio-phenological traits that impact fitness) across different habitats (Hakim et al., 2023; Leishman et al., 2014; Rathee et al., 2021), may also determine that some non-native plant species become invasive.

The phylogenetic relatedness of non-native species to the native species of a given community, a proxy for niche overlap and trait similarity (based on the integrated phenotype) (Yannelli et al., 2017), has been described as a key determinant of the success of the non-native species (Ricotta et al., 2010). In this regard, two alternative hypotheses known as Darwin's Naturalization Conundrum have been proposed to explain the successful establishment and spread of non-native species in the introduced range (Darwin, 1859; Diez et al., 2008; Thuiller et al., 2010). The preadaptation hypothesis states that non-native species phylogenetically close to natives would succeed in the introduced area, as closely related species may show similar adaptations to the environment (Darwin, 1859). In contrast, Darwin's naturalization hypothesis suggests that non-native species that are phylogenetically dissimilar to native species can establish successfully in a new region due to niche differentiation between distantly related species, which in turn may decrease competition during the invasion process (Cadotte et al., 2018; Daehler, 2001).

In plants, empirical support for both Darwin's naturalization and preadaptation hypotheses has been reported (Duncan & Williams, 2002; Loiola et al., 2018; Ordonez, 2014; Strauss et al., 2006; Thuiller et al., 2010). Naturalized non-native plant species have been documented to be more phylogenetically closely related to native species in high-latitude regions than at lower latitudes (Fan et al., 2023), highlighting the role of preadaptation in harsher climates including cold or arid regions.

Given the connection between phylogenetic and trait similarity, Darwin's naturalization hypothesis is supported by the functional divergence between native and non-native plant species reported in several studies (e.g. Funk et al., 2016; Henn et al., 2019; Ordonez et al., 2010; Petruzzellis et al., 2021). As each resource-use strategy (i.e. acquisitive or conservative) is associated with a particular set of plant functional traits (Díaz et al., 2016; Reich, 2014; Wright et al., 2004), the functional differentiation between native and non-native plant species may permit the non-native species to exploit niches that are different from those of the native species (Lambdon et al., 2008). For instance, non-native species in high-resource ecosystems or disturbed habitats tend to display functional traits related to high rates of resource acquisition and rapid growth, including higher specific leaf area (SLA), leaf nitrogen per unit mass and leaf phosphorus per unit mass compared with native plants (Leishman et al., 2007). Conversely, and in line with the preadaptation hypothesis, a conservative growth strategy can be promoted in both non-native and resident plant species by habitat filtering (e.g. cold temperatures, decreased water availability), which in turn may account for functional trait convergence between the two species groups (e.g. Dainese & Bragazza, 2012; El-Barougy et al., 2020; Grime, 2006; Gross et al., 2013). For example, conservative functional traits linked to drought resistance, such as low leaf area values, have been reported in herbaceous native and non-native species in arid ecosystems (Tecco et al., 2010). Similarly, reductions in SLA have been found in invasive and native tree species under controlled drought conditions (Schumacher et al., 2008). Both native and invasive species have also been shown to exhibit a similar increase in water-use efficiency under low water availability (Drenovsky et al., 2012).

Despite empirical evidence of the functional or phylogenetic similarity between native and non-native plant species, the joint impacts of species' phylogenetic relatedness (i.e. phylogenetic distances) and functional traits on the success of non-native plants have been less frequently studied (e.g. Loiola et al., 2018;

Ordonez, 2014; Pinto-Ledezma et al., 2020). In a research synthesis study, Ordonez (2014) reported that non-native plant species were phylogenetically similar, but functionally dissimilar to the incumbent native community. Similarly, Pinto-Ledezma et al. (2020) found that co-occurring native and non-native plant species were phylogenetically closely related, except at the ends of a fire-frequency gradient. This study also showed that the two species groups were functionally similar in communities subject to high fire frequency, thereby emphasizing the influence of the environmental context on the functional and phylogenetic aspects of the relationship between native and non-native plant species.

High-elevation habitats, such as those found above the natural tree line (i.e. alpine habitats), are characterized by low temperatures, high solar irradiance, unstable substrates and short growing seasons (Körner, 2007, 2021). In these habitats, native plant species mostly show conservative functional traits, including low leaf area and SLA, and greater leaf thickness and leaf dry matter content (LDMC), in response to the environmental harshness (Cruz-Maldonado et al., 2021; Jin et al., 2024; Ke et al., 2022; Körner et al., 1986). Although the harsh environmental conditions that characterize high-elevation areas were thought to constrain plant invasions (Pauchard et al., 2009), some non-native plants have been demonstrated to establish successfully in these environments in mountains around the world (e.g. Alexander et al., 2011; McDougall et al., 2011; Pauchard et al., 2009; Yang et al., 2018), leading to a homogenization of plant communities along elevational gradients (Haider et al., 2018). The successful establishment of non-native plants in high-elevation ecosystems may be favoured by the development of functional traits that promote a conservative growth strategy (Alexander et al., 2009; Haider et al., 2012) or preadaptations to these extreme environments (Daehler, 2005), thus supporting the preadaptation hypothesis. However, in these habitats, some non-native plant species showing functional traits that differ from those of native plants (Darwin's naturalization hypothesis) can be present (e.g. Ahmad et al., 2023; Dolezal et al., 2019). This might be related to microenvironmental changes driven by anthropogenic disturbances (Lembrechts et al., 2016; Marini et al., 2012) and/or facilitation by native nurse plants (Badano et al., 2007; Cavieres et al., 2005).

Mountains in Mediterranean-type climate zones such as the Andes of central Chile have opposite elevational gradients of water availability and temperature, with summer drought exerting a strong influence at low elevations, while alpine habitats are affected by low-temperature stress (Cavieres et al., 2006; Schöb et al., 2013). In central Chile, habitats below the tree line are dominated by sclerophyllous species (Armesto et al., 2007), highlighting the role of summer drought on plant community structure, as species with a high degree of sclerophylly can exhibit mechanisms of drought resistance (Lo Gullo & Salleo, 1988). Despite the stressful environmental conditions described for the central Chilean Andes, non-native plant species have been found in this mountainous area, especially along roadsides (Alexander et al., 2011; Haider et al., 2018; Tellier et al., 2011), where the number of non-native species has been shown to be higher (Haider et al., 2018). Some of these species have been classified as invasive, including *Cerastium arvense* and *Taraxacum officinale* (Badano et al., 2007). Thus, the Andes of central Chile provides the opportunity to examine the impacts of steep environmental gradients of temperature and soil water availability (1200–3600 m) on both the functional and phylogenetic similarity between native and non-native species. However, to date, only a few studies have assessed the effects of elevational gradients in the central Chilean Andes on leaf functional traits, the surveys being mostly focused on the responses of native species occurring in alpine habitats (López-Angulo et al., 2018; Schroeder et al., 2024; Seguí et al., 2018).

Here, we evaluated the functional and phylogenetic similarity between coexisting native and non-native species in roadside habitats along a wide elevational gradient (from 1200 to 3600 m a.s.l.) in the central Chilean Andes. Furthermore, we analysed the variation in individual leaf traits in the two species groups along the elevational gradient as well as trait covariation. Based on the above context, we tested the following hypotheses:

> **H1.** If low-elevation drought and high-elevation cold temperatures (above the tree line) in the Andes of central Chile promote a conservative resource-use strategy in co-occurring native and non-native plant species, both the phylogenetic and the functional distances between the two species groups are expected to be reduced under these harsh environmental conditions (Figure 1). These assumptions are in accordance with the preadaptation hypothesis.

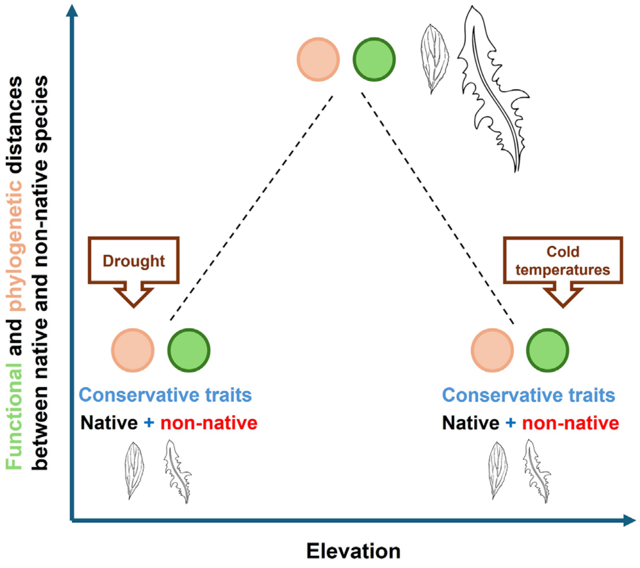


FIGURE 1 Expectations for changes in functional and phylogenetic distances of non-native plant species relative to native species along an elevational gradient. These distances are predicted to be reduced in low-elevation areas subject to drought and in alpine habitats subject to cold temperatures (preadaptation hypothesis). For both native and non-native species, we expected conservative functional traits in these harsh environments.

H2. Conservative functional traits including low leaf area and SLA, and increased LDMC and leaf thickness, are predicted to be found in both native and non-native plant species from alpine habitats and low-elevation Andean areas subject to drought, thus accounting for functional trait convergence (Figure 1).

2 | METHODS

2.1 | Study area

Sampling was conducted in roadside habitats at elevations of 1200, 1600, 2100, 2400, 3100 and 3600 m a.s.l. in the central Chilean Andes (Figure S1). In this mountain region, roadside habitats exhibit a higher number of non-native plant species compared to habitats away from roads (Haider et al., 2018). Leaf collection was conducted during the peak of the growing season (i.e. most individuals flowering) of each of the six elevational zones to ease plant identification. At the tree line and in alpine habitats, leaves were collected during the growing season of November 2019–March 2020, while leaf sampling at elevations below the tree line occurred in September 2020. No permits were required for fieldwork.

Central Chile has a Mediterranean-type climate, with summer drought mostly influencing low-elevation sites (di Castri & Hajek, 1976). Accordingly, in central Chile, Andean ecosystems at 1600 m a.s.l. are characterized by lower soil water contents compared with those described for higher elevations (3600 m a.s.l.) (Reyes-Bahamonde et al., 2022).

The closest climate station to the lowest study site (1200 m a.s.l.) is San José Guayacán (928 m a.s.l.) where the mean annual precipitation was 195.5 mm between 2018 and 2020, while the growing season's mean temperature was 20.9°C in 2020, with minimum and maximum temperatures of 15.1 and 24.3°C, respectively (source: Chile's national weather service). In central Chile, at 1600 m a.s.l., the historical mean annual precipitation is 445 mm, falling predominantly as rain during the winter months (Santibáñez & Uribe, 1990). At this elevation, the mean temperature at the end of the growing season was 13.1°C in 2011, ranging from 10.6 to 22.5°C (Hernández-Fuentes et al., 2015). In the high Andean zone of central Chile, at 3600 m a.s.l., the historical mean annual precipitation has been described to be 943 mm, falling mainly as snow in winter, with occasional hail or snowfall in summer (Santibáñez & Uribe, 1990). At this elevation, the mean temperature at the end of the growing season was 8.2°C in 2011, with minimum and maximum temperatures of −1.0 and 20.1°C, respectively (Hernández-Fuentes et al., 2015).

Along the elevational gradient, different vegetation types were recorded, including Mediterranean sclerophyllous scrub at 1200 m, where native woody species such as *Quillaja saponaria* and *Kageneckia oblonga* are abundant, montane sclerophyllous woodland dominated by *K. angustifolia* at 1600 m (Arroyo et al., 2002), and alpine vegetation above the tree line (2100–2200 m), dominated by prostrate shrubs between 2100 and 2600 m, and by cushion and rosette plants from 2600 to 3600 m (Cavieres et al., 2000).

2.2 | Functional trait measurements

At each elevation, we established a single plot of 50 × 2 m, which was adjacent to the road. All the vascular plant species occurring in these plots were recorded. For trait measurements, only the plant species present in the plots were considered. For some of these species, there were not enough individuals in the sample plots, due to which a greater area (proximate to the road) was sampled per elevation (Figure S1) to obtain sufficient leaf samples for all the study species (Table S1). Species' biogeographic origin was determined according to Tellier et al. (2011).

We measured on native and non-native species the following functional traits: leaf area, SLA, LDMC, leaf thickness and the contents of leaf nitrogen and chlorophyll. For most of the plant species found at each elevation, 8–10 mature individuals were randomly chosen for leaf collection. For species that were less frequent in the study area, five or six individuals were selected. For each plant, one fully expanded and mature leaf was randomly chosen. Additional leaves were sampled from individuals of species with small and light leaves to obtain sufficient leaf biomass for the determination of SLA and LDMC. The leaves were cut and immediately wrapped in a moist paper towel and placed in individual sealed aluminium foil paper bags. The samples were stored in a portable cooler until processing. Following the protocol described by Pérez-Harguindeguy et al. (2016), within 24 h after leaf sampling, leaf thickness, leaf fresh mass, leaf area and chlorophyll content were determined. Leaf thickness and chlorophyll content were measured on leaves of five or six individuals per species and elevation. Chlorophyll content was determined using a portable chlorophyll content meter (CCM-300, Opti-Sciences). The fresh mass (g) of the selected leaves (excluding petioles) was measured with an electronic microbalance (weight uncertainty ±1 μg). A digital calliper was used for measuring the thickness of each leaf blade (mm). Next, the leaves were flattened and scanned with a flatbed scanner. The ImageJ software was used for measuring leaf area. Subsequently, the leaves were oven-dried for 72 h at 60°C, and the final dry mass (g) was measured with an electronic microbalance. For the determination of leaf nitrogen content (% of dry weight), leaf samples of four individuals per study species were dried in silica gel and transported to the laboratory of biogeochemical analysis at the Pontificia Universidad Católica, Chile. LDMC was calculated as the ratio of dry weight to fresh weight, while SLA was determined by dividing leaf area by leaf dry weight. Plant height was also measured, from the stem base to the upper boundary of the main photosynthetic tissues (excluding inflorescences).

2.3 | Functional and phylogenetic distances

To assess the functional and phylogenetic similarity of non-native plant species relative to the native communities along the elevational gradient, we calculated the functional and phylogenetic distances between the two species groups.

A phylogenetic tree including 116 angiosperm species recorded along the elevational gradient (Figure S2) was built with the phylo.maker function of the R package 'V.PhyloMaker' (Jin & Qian, 2019). The time-calibrated megaphylogeny for vascular plants 'GBOTB.extended.tre', which includes 74,533 species, was used as a backbone (Jin & Qian, 2019). One of the study species (*Adesmia mucronata*; Table S1) was absent from the mega-tree. As a result, this species was only considered for the functional similarity analysis (see description below). To generate the phylogeny, we used the scenario in which missing genera or species were joined to the half-way point of the family/genus branch (Scenario 3). An interspecific phylogenetic distance matrix was obtained with the cophenetic function in the picante package for R (Kembel et al., 2010). For each elevation, the phylogenetic distances from some of the non-native species to most of the native species were equal (Figure S4). Due to this, we considered a focal-species approach, which enables evaluating the phylogenetic relatedness of each non-native species to the native species in a community (Pinto-Ledezma et al., 2020). Thus, for each elevation, the mean phylogenetic distances of focal non-native species relative to the native species were calculated (MPD focal). These phylogenetic distances were obtained for all the non-native species recorded.

Based on a matrix of the six leaf traits measured in our study species, a functional distance matrix was constructed using Euclidean distances. Prior to calculating the functional distances, the leaf traits were scaled to zero mean and unit variance. Using the functional distance matrix as input, we calculated the mean functional distance between each non-native plant species and all native species it co-occurs (MFD focal), as proposed by Ordonez (2014).

2.4 | Phylogenetic signal

To determine whether the morphological leaf traits and chlorophyll content were influenced by phylogeny, we tested for a phylogenetic signal in these traits. Phylogenetic signal was not evaluated for leaf nitrogen content as this trait may be greatly affected by soil nutrient availability. For each trait, we estimated Blomberg's K and Pagel's λ (Pagel, 1994), using the function phylosig (package phytools; Revell, 2012) and the phylogenetic tree for 116 study species described above. Mean trait values for each species were used (considering samples from all the elevations where the species were present).

2.5 | Statistical analyses

We performed generalized linear models (GLMs) and likelihood-ratio tests to evaluate the effect of elevation on the mean phylogenetic and functional distances between native and non-native species. Elevation was considered a categorical factor (four levels: 1200, 1600, 2100 and 2400 m a.s.l.). For GLMs, Gamma error structure and log link function were used. Due to the small number of non-native species recorded above 3000 m ($N = 2$), the phylogenetic and functional distances calculated for these two focal species were not included in the GLMs. The models were conducted using the R stats package and checked for over-dispersion by inspecting both residual deviance and residual degrees of freedom. Homogeneity of variance was checked visually using plots of standardized residuals versus fitted values.

The effects of elevation and biogeographic origin of species (native or non-native) on five leaf traits were analysed using linear mixed-effects models (LMMs). We performed a negative binomial generalized linear mixed model (GLMM) to examine the effect of the two predictors on chlorophyll content. In the mixed models, species identity was included as a random effect. Most of the response variables were log-transformed to reduce deviation from normality. Model quality was assessed by Akaike information criterion (AIC) values. To do so, models consisting of full combinations of fixed factors and interaction terms were tested, and significance values are reported here for the best model for each trait (Table 2). Normality of residuals was checked visually through histograms of normalized residuals, and by conducting Shapiro–Wilk normality tests. The residuals versus fitted values were plotted in order to check for homoscedasticity. The variance explained by the full model (conditional R^2) was calculated using the R package 'MuMIN' (Bartoń, 2023). *p*-values were obtained from F-statistics of type III sum of squares with the Satterthwaite approximation to estimate the denominator degrees of freedom. For the GLMM, a likelihood ratio test was used to calculate *p*-value. The linear mixed models and the GLMM were carried out using the R package 'lme4' (Bates et al., 2015). Multiple comparisons were performed using Tukey's post hoc tests in the R package 'emmeans' (Lenth, 2022).

We conducted a principal component analysis (PCA) on the dataset of six leaf functional traits to identify major axes of trait co-variation and determine the trait spaces for native and non-native species. Mean trait values for each species and elevation were considered. The traits were scaled to zero mean and unit variance. Randomization tests with the 'rank-of-roots' statistic (percentage of explained variance) were used to select significant PC axes (Camargo, 2022). All permutation-based statistical tests (1000 random permutations) were performed using the R package 'PCAtest' (Camargo, 2022). All analyses were conducted in the R statistical software (v. 4.2.1; R Core Team, 2022).

3 | RESULTS

A total of 117 plant species were identified in roadside habitats along the elevational gradient (91 natives and 26 non-natives). Asteraceae ($N = 27$ species) and Poaceae ($N = 13$ species) were the most represented families (Table S1). Below the tree line, at 1200 and 1600 m, native species included perennial herbs ($N = 7$ species),

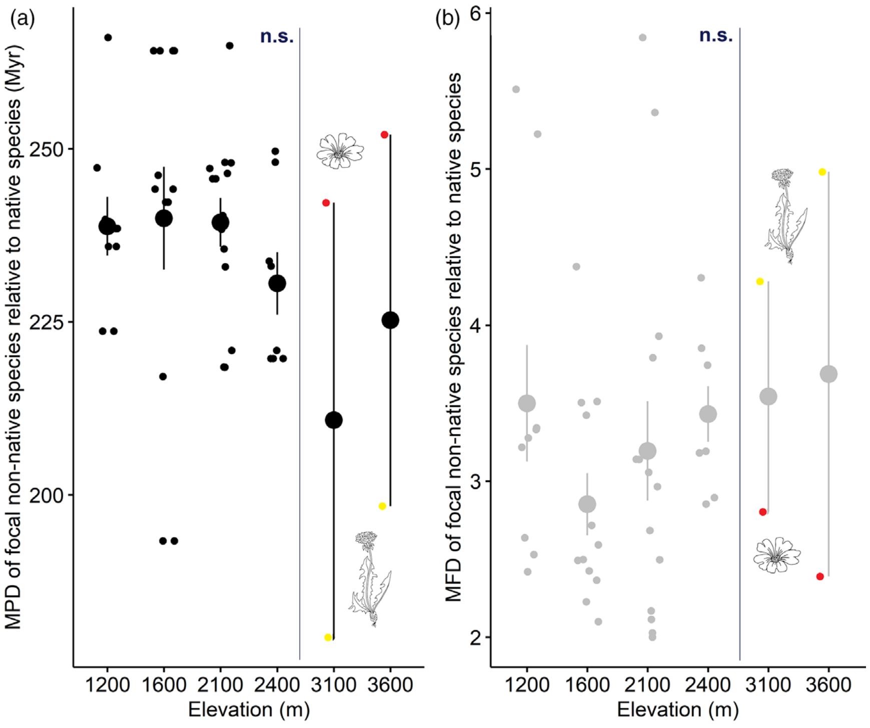


FIGURE 2 Mean phylogenetic (a) and functional (b) distances of non-native plant species relative to their co-occurring native species along an elevational gradient. Means (±SEM) per elevation are also shown. n.s. = no significant differences between means (from 1200 to 2400 m). The functional and phylogenetic distances calculated for the two non-native species found above 3000 m are indicated by dot colour: Red (*Cerastium arvense*) and yellow (*Taraxacum officinale*).

annual herbs (N = 14), shrubs (N = 6 species) and two tree species. In contrast, most of the non-native species below the tree line were annual herbs (N = 15), with only two perennial herbs recorded in this species group (Figure S3). At higher elevational sites (3100 and 3600 m), most of the native species were perennial herbs (N = 22). At these elevations, four native shrubs and four native annual herbs were also found. Only two non-native species, the perennial herbs *Cerastium arvense* and *Taraxacum officinale*, were present in the sampling areas above 3000 m.

3.1 | Functional and phylogenetic similarity between native and non-native species

The mean phylogenetic and functional distances between native and non-native plant species did not vary significantly along the elevational gradient (from 1200 to 2400 m; Figure 2; Table 1; Table S2). Above 3000 m, *T. officinale* (yellow circles; Figure 2a) was more phylogenetically related to the native communities than *C. arvense* (red circles; Figure 2a). However, *T. officinale* was functionally divergent from the native members of the high-elevation plant communities (yellow circles; Figure 2b), in contrast to *C. arvense* (red circles; Figure 2b).

TABLE 1 Likelihood ratio test comparing main-effect model with intercept-only model. Mean phylogenetic and functional distances between native and non-native plant species were modelled as a function of elevation site (1200, 1600, 2100 and 2400 m a.s.l.) using generalized linear models.

Model	Resid. deviance	LR-test statistic	df	*p*
Mean phylogenetic distance[a]				
Null	0.219			
Elevation	0.229	1.728	3	0.631
Mean functional distance[a]				
Null	3.050			
Elevation	3.316	3.028	3	0.387

Abbreviation: df, degrees of freedom; LR, Likelihood ratio.

[a] Gamma error structure (link = log).

3.2 | Leaf trait variation along the elevational gradient

For most of the functional traits considered in our study, non-native plant species showed responses to elevation that differed from those of native species (Figures 3 and 4). On average, the non-native species were characterized by acquisitive leaf traits. For instance, along most of the elevational gradient (including habitats above the tree line), the non-native species exhibited greater leaf area than the native species (Figure 3; Table 2; Table S3). At half of the elevations studied, the non-native species also had higher mean SLA values compared with those of native species (Figure 3; Table 2; Table S3). Habitats above the tree line were also characterized by the presence of non-native species with lower LDMC (Figure 3) and higher leaf nitrogen per unit mass (Figure 4; Table 2; Table S3) in comparison with native species. However, chlorophyll content (Figure 4; Table S3) and leaf thickness (Figure 3; Table 2) did not vary between the species groups along the elevational

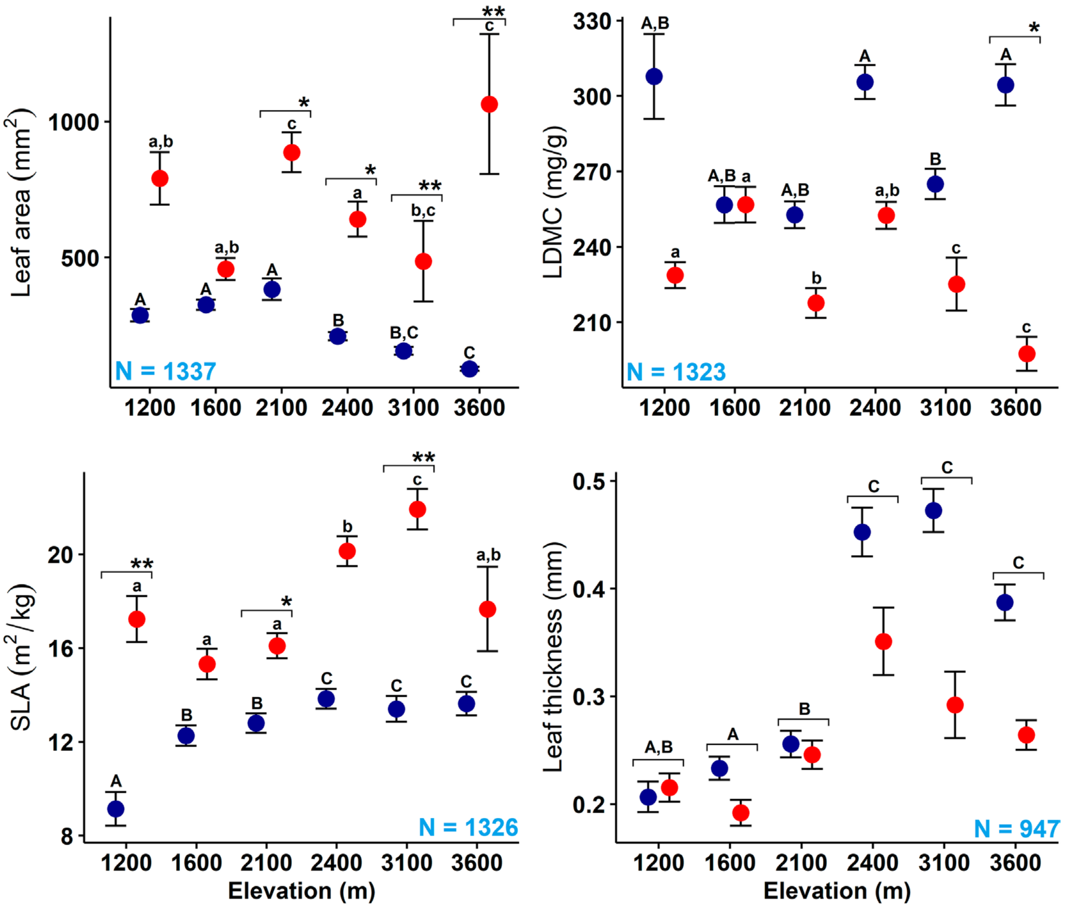


FIGURE 3 Variation in leaf morpho-anatomical traits of native (blue circles) and non-native (red circles) species along an elevational gradient. Mean values (±SEM) are shown. For linear mixed-effects models, the traits were log-transformed. LDMC, leaf dry matter content; SLA, specific leaf area. For each elevation, statistically significant differences between means for native and non-native species at $^*p<0.05$ and $^{**}p<0.0001$ are indicated (according to Tukey's post hoc tests; Table S3). For each species group, the mean values of a particular trait with distinct letters differed significantly (Tukey's post hoc tests; $p<0.05$).

gradient. Greater leaf thickness was recorded in both native and non-native species in alpine habitats (Figure 3; Table 2).

For native species, leaf area decreased significantly from 2400 m (above the tree line) to the upper elevational end (Figure 3; Table 2). In contrast, for non-native species, the high mean values of leaf area obtained from the samples collected at the tree line (2100 m) did not differ from those of the leaves sampled above 3000 m (Figure 3; Table 2). For non-native species, SLA did not vary between the lowest elevational limit and the tree line (Figure 3; Table 2). However, for the two species groups, SLA increased significantly in habitats above the tree line (Tukey's post hoc tests, $p<0.0001$; Figure 3; Table 2). For all the traits measured in our study (Figures 3 and 4), the random factor 'species identity' influenced the observed relationships (Table 2).

In the PCA including chlorophyll content, leaf area, LDMC, leaf nitrogen content (% of dry weight), leaf thickness and SLA, the first two axes accounted for 33.4% and 21.2% of the total variation among species, respectively (Figure 5). According to randomization tests, the first two PCs were significant ($p<0.05$).

The spread of the leaf samples along PC1 and PC2 indicates that the variation in the functional traits of the study species was mostly gradual along the elevational gradient (Figures 5 and 6). Leaf nitrogen content (N), LDMC and SLA were the most important contributors to the first PC, while the second axis was mainly associated with leaf thickness and chlorophyll content (Figure 5). Below the tree line (2100 m), the native species exhibited a gradient of functional responses running from conservative (high LDMC) to acquisitive (high N and leaf area), whereas the non-native plant species mostly showed acquisitive leaf traits along the elevational gradient (Figure 5). The native species from higher elevations (2400–3600 m) and some of the non-native species occurring in alpine habitats had greater leaf thickness (Figure 5). The non-native species studied here showed a smaller total trait space compared with that of the native species (Figure 5a). The trait spaces of the native species found at 1200 m, 2400 m and above 3000 m were larger than those of the non-native species occurring at these elevations, as indicated by the convex hull areas per species groups (Figure 6).

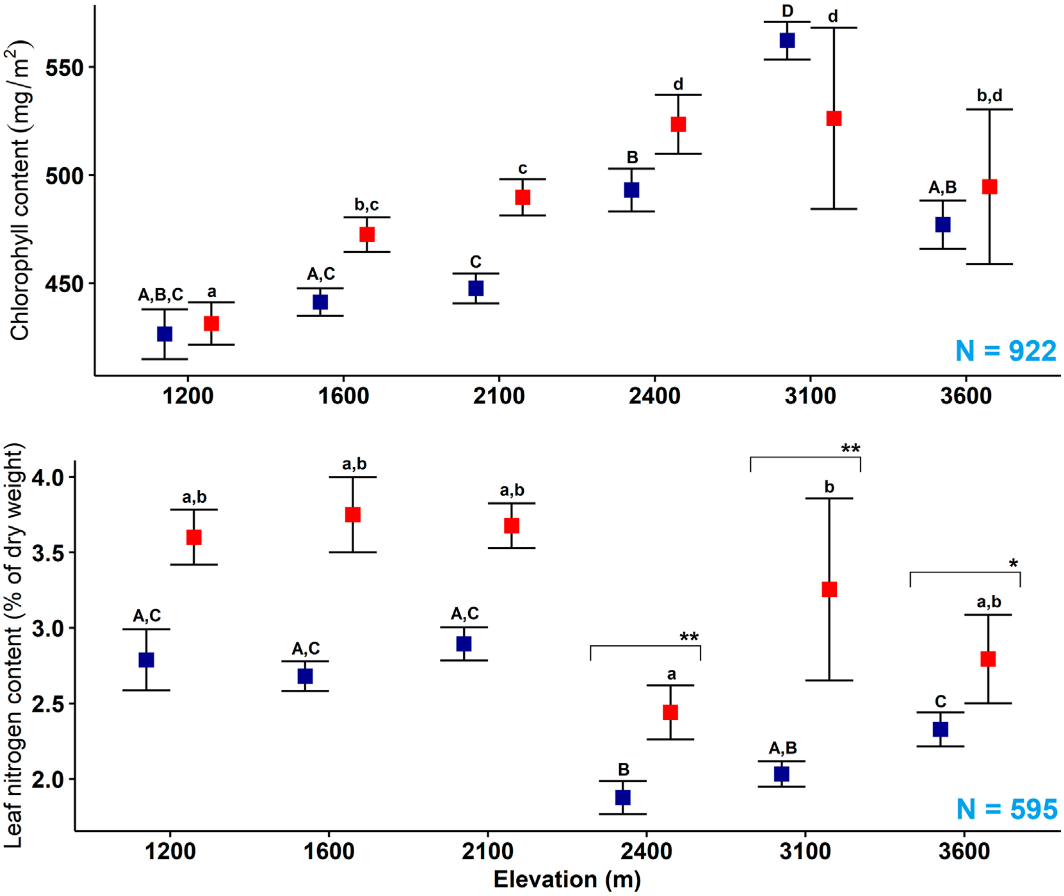


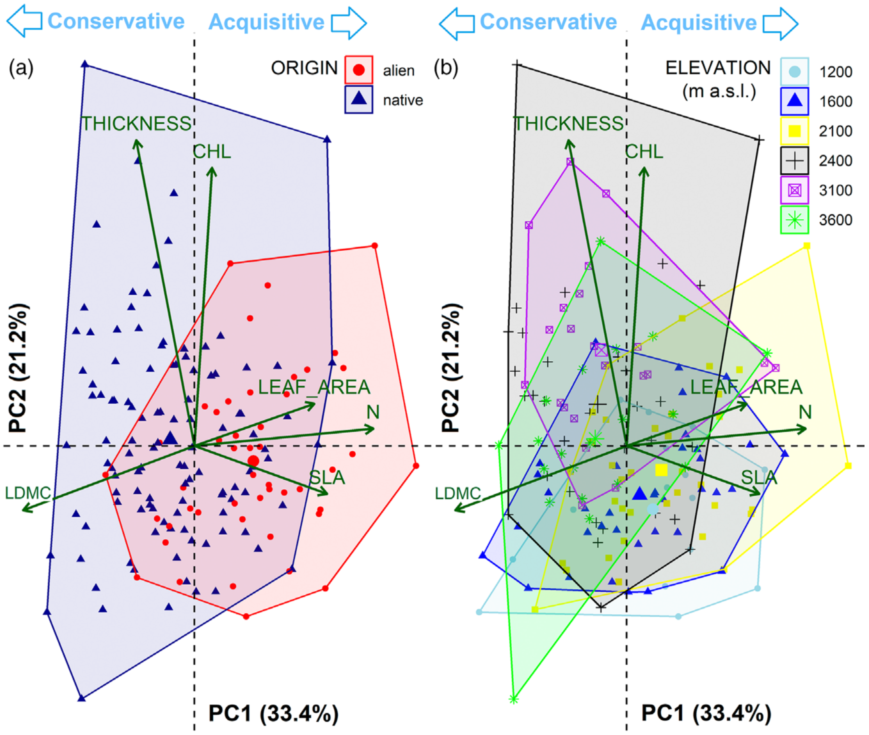
FIGURE 4 Variation in chlorophyll content and leaf nitrogen content (% of dry weight) of native (blue squares) and non-native (red squares) species along an elevational gradient. Mean values (±SEM) are shown. For the linear mixed-effects model, leaf nitrogen content was log-transformed. For each elevation, statistically significant differences between means for native and non-native species at $^*p < 0.05$ and $^{**}p < 0.0001$ are indicated (according to Tukey's post hoc tests; Table S3). For each species group, the mean values of a particular trait with distinct letters differed significantly (Tukey's post hoc tests; $p < 0.05$).

TABLE 2 Linear mixed models testing for the effects of elevation and biogeographic origin (native or non-native) on five leaf traits (log-transformed).

	Fixed effects										
	Elevation			Biogeographic origin			Elevation × B. origin				
Traits	df	*F*	*p*	df	*F*	*p*	df	*F*	*p*	R^2_m	R^2_c
Leaf area[a]	1268.4	13.83	<0.001	130.0	31.23	<0.001	1268.4	16.48	<0.001	0.314	0.850
Leaf N[a]	547.5	8.69	<0.001	133.1	22.99	<0.001	547.5	3.35	<0.01	0.217	0.793
Leaf thickness[a]	910.2	15.66	<0.001	112.8	4.52	<0.05				0.189	0.859
LDMC[a]	1267.2	8.35	<0.001	125.8	6.70	<0.05	1267.2	6.68	<0.001	0.044	0.832
SLA[a]	1270.0	38.14	<0.001	125.4	25.61	<0.001	1270.0	22.15	<0.001	0.233	0.862
							df	χ^2	*p*		
Chlorophyll content							11	140.52	<0.001	0.194	0.742

Note: *F*-values and *p*-values were obtained from type III sum of squares with the Satterthwaite's method to estimate the denominator degrees of freedom (df)[a]. For chlorophyll content, a generalized linear mixed model (GLMM) including the two predictor variables and the interaction term was conducted (negative binomial error structure). For leaf thickness, the best-fit model (lowest Akaike information criterion) excluded the interaction effect. Species identity was included in the models as a random factor. For each model, the marginal R^2 (variance explained by the fixed factors) and the conditional R^2 (variance explained by the full model) are given. A likelihood ratio test was used to compare the GLMM for chlorophyll content with an intercept-only model.

FIGURE 5 Principal component analysis of six leaf traits for 117 plant species ($N = 161$ observations) found along an altitudinal gradient (from 1200 to 3600 m) in the central Chilean Andes. Ordination diagrams of the first (PC1) versus the second (PC2) principal components are presented (a, b). Convex hulls for species group (a) and elevation (b) are shown. CHL, chlorophyll content (mg/m^2), leaf area (mm^2); LDMC, leaf dry matter content (mg/g), N, leaf nitrogen content (% of dry weight), leaf thickness (mm) and SLA, specific leaf area (m^2/kg).



3.3 | Phylogenetic signal

We did not find a phylogenetic signal for most of the functional traits studied (lambda and *K* values close to zero; Table S4). Only LDMC was subject to a significant phylogenetic signal (Table S4).

4 | DISCUSSION

Knowledge of the functional and phylogenetic similarity between native and non-native plant species along environmental gradients is central to understanding plant invasions (Divíšek et al., 2018; Henn et al., 2019; Ordonez, 2014; Qian & Sandel, 2017). We expected reduced functional and phylogenetic distances between these two groups of plants in low-elevation areas influenced by marked drought and in alpine habitats in the Andes of central Chile. Therefore, these assumptions were consistent with the preadaptation hypothesis (i.e. non-native species closely related to natives would establish successfully in a new region). However, contrary to our predictions, we found no significant effect of elevation on the functional and phylogenetic distances between native and non-native plant species in the central Chilean Andes, thereby suggesting that these distances were unaffected by harsh environmental conditions in this mountainous area. Thus, the preadaptation hypothesis, assessed by either the functional or the phylogenetic similarity between two species groups, would not be supported by our study. In contrast, no reductions in the phylogenetic distances between native and non-native plant species in harsh Andean environments might be indicative of phylogenetic dissimilarity between the two species groups in these habitats, thus supporting Darwin's naturalization hypothesis.

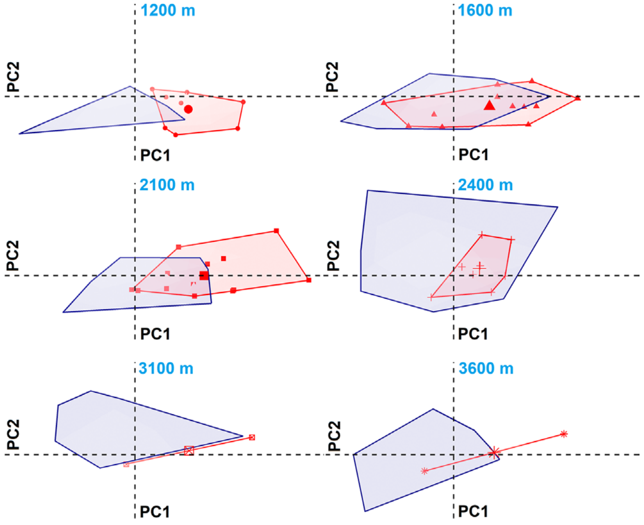


FIGURE 6 Convex hulls for native (blue colour) and non-native (red colour) plant species occurring along an elevational gradient in the Andes of central Chile. Six leaf functional traits of 117 species were considered. $N = 161$ observations.

In line with our findings, some studies have evidenced phylogenetic dissimilarity of non-native plant species to co-occurring natives under stressful environmental conditions. For example, non-native plant species less related to natives have been reported in some ecosystems affected by summer drought (Strauss et al., 2006). Similarly, in plant communities under drought conditions, the cover of the invasive species *Ageratina adenophora* has been shown to be negatively influenced by the invader-resident phylogenetic relatedness (Wang et al., 2024).

We predicted conservative functional traits in both native and non-native plant species due to low-elevation drought and high-elevation cold temperatures (alpine habitats) in the Andes of central Chile. However, in opposition to our assumptions, increased leaf thickness was the only conservative trait found in both native and non-native species in harsh Andean environments (alpine habitats). We recorded other conservative functional traits in native species such as those that exhibited low leaf area values in high-elevation habitats or a reduced SLA in low-elevation areas exposed to marked summer drought, as described for other water-limited environments (Pérez-Ramos et al., 2012). Conversely, along most of our elevational gradient, the non-native species were characterized by greater values of leaf area compared with those reported in the native species, even in alpine habitats. Additionally, the non-native species showed higher SLA than the native species at half of the elevations considered in our study (including an alpine site and an area influenced by drought). Above the tree line, the non-native species studied here also presented higher leaf nitrogen content per unit mass (e.g. Kühn et al., 2021) and lower LDMC than the native species. All in all, the leaf trait combinations that characterized the non-native plant species along our elevational gradient suggest an acquisitive growth strategy for these species, thus supporting the acquisitive leaf traits described for non-native plants in research syntheses (e.g. Leishman et al., 2007; Ordonez et al., 2010). Most of the leaf traits evaluated in our study (except for LDMC) would have evolved independently of any phylogenetic effects, as suggested by the lack of relationship between the trait values and the phylogeny of the studied species.

The functional dissimilarity between native and non-native plant species evidenced in Andean habitats of central Chile, including those exposed to drought or low temperatures, may facilitate the establishment and spread of non-native species in this mountainous region by promoting niche differentiation between the two species groups (Darwin's naturalization hypothesis), particularly in roadside habitats, which might be subject to anthropogenic disturbances. Non-native species showing traits linked to rapid resource acquisition in the roadside habitats studied could be favoured by a promotive effect of disturbance on resource availability, as reported in some disturbed habitats (e.g. Leishman et al., 2007). Alternatively, in environmentally severe habitats in the central Chilean Andes, the presence of non-native plant species functionally and/or phylogenetically dissimilar to native species might be explained by the amelioration of these extreme abiotic conditions by nurse plants (Cavieres, 2021). Plant facilitation has been demonstrated to occur primarily between distantly related species (Valiente-Banuet & Verdú, 2007; Verdú et al., 2012; Zhang et al., 2016). Facilitation between distantly related plant species has also been found in the Andes of central Chile, below the tree line (from 1000 to 2000 m; Duarte et al., 2021).

The establishment of the two non-native plant species that we found in high-Andean habitats (*Cerastium arvense* and *Taraxacum officinale*) has been shown to be promoted by native cushion plants (Badano et al., 2007; Cavieres et al., 2005). Cushion plants are well known for providing microhabitats with milder temperatures and higher soil moisture, which facilitate the growth and survival of the species growing within the cushions (Cavieres et al., 2005, 2006). In the high-elevation areas considered in our study, *C. arvense* was found to be phylogenetically dissimilar to the native communities, while *T. officinale* was phylogenetically close to the native species. Interestingly, in these harsh environments, *T. officinale* was functionally different from the native members of the evaluated communities, as this non-native species exhibited acquisitive leaf characteristics, thus highlighting the role of facilitative interactions. Some studies have documented the contribution of stress amelioration by nurse species to the development of an acquisitive growth strategy in facilitated plants. For instance, in herbaceous species inhabiting areas under water stress, acquisitive functional traits including higher leaf area and SLA have been shown to be favoured by nurse plants (García-Cervigón et al., 2015). Similarly, in the Himalayas, plant species colonizing alpine cushions have been described as functionally distinct from alpine plant species growing in bare soil (Dolezal et al., 2019).

In our study, all the non-native species from 1600 m a.s.l. (below the tree line) exhibited an annual life-history strategy, which might also promote an acquisitive resource-use strategy in these species, as described for annual plants that escape soil moisture depletion (Brouillette et al., 2014). Annuals have been found to present higher SLA compared to perennials (Garnier et al., 1997). Thus, leaf attributes related to high resource acquisition could be linked to the prevalence of invasive annuals in some Mediterranean-type climate regions (Funk et al., 2016). Hence, further research on the potential influence of the plant life cycle on the functional traits of the studied species in central Chile, under controlled environmental conditions, is required.

The prevalence of leaf traits related to faster resource acquisition in non-native species exposed to stressful conditions in the Andes of central Chile (drought or low-temperature stress) suggests that the growth strategy and the proliferation of these species could be highly dependent on the modification of the environment by nurse plants and/or a high degree of disturbance. Nevertheless, the successful spread of non-native species towards alpine habitats might be constrained not only by facilitative interactions and/or anthropogenic disturbances but also via the development of some conservative functional responses. Supporting this idea, we recorded increased leaf thickness in non-native species inhabiting alpine areas of central Chile, including *T. officinale*, compared to low-elevation non-native species. This conservative trait response in *T. officinale* could contribute to freezing resistance, at similar levels as native species, as evidenced at 2900 and 3600 m a.s.l. in the central Chilean Andes (Sierra-Almeida et al., 2009). Additional research on the potential effects of plant facilitation and disturbance on the leaf functional traits of the native and non-native species studied here, as well as the exposure of these plants to water or low-temperature stress under controlled environmental conditions, would be required to determine the explanatory mechanisms behind the trait composition determined for Andean plant communities in central Chile.

Our study provides novel insights into the functional and phylogenetic similarity between native and non-native plant species occurring in roadside habitats along an elevational and water availability gradient in the Andes of central Chile, a topic previously unexplored in this mountain region influenced by a Mediterranean-type climate. Functional differentiation of non-native plant species from the native community was evidenced in habitats under the influence of summer drought (below the tree line) or cold temperatures (alpine areas), instead of functional convergence between the species groups as expected under strong habitat filtering. Furthermore, the phylogenetic distances between co-occurring native and non-native plant species were reported to be similar along the elevational gradient, thereby suggesting the establishment of some non-native plant species less related to the resident species in abiotic stressful environments of the central Chilean Andes. Overall, our findings support Darwin's naturalization hypothesis instead of the preadaptation hypothesis.

AUTHOR CONTRIBUTIONS

Lohengrin A. Cavieres, Patricia L. Sáez, Aníbal Pauchard and León A. Bravo conceived the project. Lohengrin A. Cavieres, Maritza Mihoč, Graciela Valencia and Claudia Reyes-Bahamonde conducted the sampling and measured the functional traits. Vinka Anic analysed the data and wrote the original draft of the manuscript. Vinka Anic, Lohengrin A. Cavieres, Patricia L. Sáez and Aníbal Pauchard contributed to subsequent revisions.

ACKNOWLEDGEMENTS

This study was funded by Chilean National Agency for Research and Development (ANID) projects: ACT210038, FB210006, FONDECYT 1211197 and FONDECYT 1211231.

CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

Our data are available from the Figshare data repository: https://doi.org/10.6084/m9.figshare.29226134.v2 (Anic et al., 2025).

ORCID

Vinka Anic https://orcid.org/0000-0002-6944-0691

Lohengrin A. Cavieres https://orcid.org/0000-0001-9122-3020

REFERENCES

Ahmad, M., Uniyal, S. K., Sharma, P., Rathee, S., Batish, D. R., & Singh, H. P. (2023). Enhanced plasticity and reproductive fitness of floral and seed traits facilitate non-native species spread in mountain ecosystems. *Journal of Environmental Management*, *348*, 119222.

Alexander, J. M., Edwards, P. J., Poll, M., Parks, C. G., & Dietz, H. (2009). Establishment of parallel altitudinal clines in traits of native and introduced forbs. *Ecology*, *90*(3), 612–622.

Alexander, J. M., Kueffer, C., Daehler, C. C., Edwards, P. J., Pauchard, A., Seipel, T., & & MIREN Consortium. (2011). Assembly of non-native floras along elevational gradients explained by directional ecological filtering. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(2), 656–661.

Anic, V., Mihoč, M., Valencia, G., Reyes-Bahamonde, C., Bravo, L. A., Sáez, P. L., Pauchard, A., & Cavieres, L. A. (2025). Data from: Functional and phylogenetic similarity between native and non-native plant species along an elevational gradient in the central Chilean Andes: No evidence for the preadaptation hypothesis. *Figshare*. https://doi.org/10.6084/m9.figshare.29226134.v2

Armesto, J. J., Arroyo, M. T. K., & Hinojosa, L. F. (2007). The Mediterranean environment of central Chile. In T. T. Y. Veblen, R. Kenneth, & A. R. Orme (Eds.), *The physical geography of South America* (pp. 184–199). Oxford University Press.

Arroyo, M. T. K., Marticorena, C., Matthei, O., Muñoz, M., & Pliscoff, P. (2002). Analysis of the contribution and efficiency of the Santuario de la Naturaleza Yerba Loca, 33° S, in protecting the regional vascular plant flora (Metropolitan and Fifth regions of Chile). *Revista Chilena de Historia Natural*, *75*, 767–792.

Badano, E. I., Villarroel, E., Bustamante, R. O., Marquet, P. A., & Cavieres, L. A. (2007). Ecosystem engineering facilitates invasions by exotic plants in high-Andean ecosystems. *Journal of Ecology*, *95*(4), 682–688.

Bartoń, K. (2023). *MuMIn: Multi-model inference*. R package Version 1.47.5. https://CRAN.R-project.org/package=MuMIn

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48.

Brouillette, L. C., Mason, C. M., Shirk, R. Y., & Donovan, L. A. (2014). Adaptive differentiation of traits related to resource use in a desert annual along a resource gradient. *New Phytologist*, *201*, 1316–1327.

Cadotte, M. W., Campbell, S. E., Li, S.-P., Sodhi, D. S., & Mandrak, N. E. (2018). Preadaptation and naturalization of nonnative species: Darwin's two fundamental insights into species invasion. *Annual Review of Plant Biology*, *69*, 661–684.

Camargo, A. (2022). PCAtest: Testing the statistical significance of principal component analysis in R. *PeerJ*, *10*, e12967. https://doi.org/10.7717/peerj.12967

Cavieres, L. A. (2021). Facilitation and the invasibility of plant communities. *Journal of Ecology*, *109*, 2019–2028.

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. *New Phytologist*, *169*, 59–69.

Cavieres, L. A., Peñaloza, A., & Arroyo, M. T. K. (2000). Altitudinal vegetation belts in the high-Andes of central Chile (33° S). *Revista Chilena de Historia Natural*, *73*, 331–344.

Cavieres, L. A., Quiroz, C. L., Molina-Montenegro, M. A., Muñoz, A. A., & Pauchard, A. (2005). Nurse effect of the native cushion plant *Azorella monantha* on the invasive non-native *Taraxacum officinale* in the high-Andes of central Chile. *Perspectives in Plant Ecology, Evolution and Systematics*, *7*, 217–226.

Cruz-Maldonado, N., Weemstra, M., Jiménez, L., Roumet, C., Angeles, G., Barois, I., de los Santos, M., Morales-Martinez, M. A., Palestina, R. A., Rey, H., Sieron, K., Stokes, A., & Anthelme, F. (2021). Aboveground-trait variations in 11 (sub)alpine plants along a 1000-m elevation gradient in tropical Mexico. *Alpine Botany*, *131*, 187–200.

Daehler, C. C. (2001). Darwin's naturalization hypothesis revisited. *American Naturalist*, *158*, 324–330.

Daehler, C. C. (2005). Upper-montane plant invasions in the Hawaiian Islands: Patterns and opportunities. *Perspectives in Plant Ecology, Evolution and Systematics*, *7*(3), 203–216.

Dainese, M., & Bragazza, L. (2012). Plant traits across different habitats of the Italian Alps: A comparative analysis between native and alien species. *Alpine Botany*, *122*, 11–21.

Darwin, C. (1859). *On the origin of the species by means of natural selection*. Murray.

di Castri, F., & Hajek, E. (1976). *Bioclimatología de Chile*. Ediciones de la Pontificia Universidad Católica de Chile.

Díaz, S., Kattge, J., Cornelissen, J. H. C., Wright, I. J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Colin Prentice, I., Garnier, E., Bönisch, G., Westoby, M., Poorter, H., Reich, P. B., Moles, A. T., Dickie, J., Gillison, A. N., Zanne, A. E., … Gorné, L. D. (2016). The global spectrum of plant form and function. *Nature*, *529*, 167–171.

Diez, J. M., Sullivan, J. J., Hulme, P. E., Edwards, G., & Duncan, R. P. (2008). Darwin's naturalization conundrum: Dissecting taxonomic patterns of species invasions. *Ecology Letters*, *11*, 674–681.

Divíšek, J., Chytrý, M., Beckage, B., Gotelli, N. J., Lososová, Z., Pyšek, P., Richardson, D. M., & Molofsky, J. (2018). Similarity of introduced plant species to native ones facilitates naturalization, but differences enhance invasion success. *Nature Communications*, *9*, 4631.

Dolezal, J., Dvorsky, M., Kopecky, M., Altman, J., Mudrak, O., Capkova, K., Rehakova, K., Macek, M., & Liancourt, P. (2019). Functionally distinct assembly of vascular plants colonising alpine cushions suggests their vulnerability to climate change. *Annals of Botany*, *123*(4), 569–578.

Drenovsky, R. E., Khasanova, A., & James, J. J. (2012). Trait convergence and plasticity among native and invasive species in resource-poor environments. *American Journal of Botany*, *99*(4), 629–639.

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.

Duncan, R. P., & Williams, P. A. (2002). Darwin's naturalization hypothesis challenged. *Nature*, *417*, 608–609.

El-Barougy, R. F., Elgamal, I., Rohr, R. P., Probert, A. F., Khedr, A.-H. A., & Bacher, S. (2020). Functional similarity and dissimilarity facilitate alien plant invasiveness along biotic and abiotic gradients in an arid protected area. *Biological Invasions*, *22*, 1997–2016.

Fan, S.-Y., Yang, Q., Li, S.-P., Fristoe, T. S., Cadotte, M. W., Essl, F., Kreft, H., Pergl, J., Pyšek, P., Weigelt, P., Kartesz, J., Nishino, M., Wieringa, J. J., & van Kleunen, M. (2023). A latitudinal gradient in Darwin's naturalization conundrum at the global scale for flowering plants. *Nature Communications*, *14*, 6244.

Funk, J. L., Standish, R. J., Stock, W. D., & Valladares, F. (2016). Plant functional traits of dominant native and invasive species in mediterranean-climate ecosystems. *Ecology*, *97*(1), 75–83.

García-Cervigón, A. I., Linares, J. C., Aibar, P., & Olano, J. M. (2015). Facilitation promotes changes in leaf economics traits of a perennial forb. *Oecologia*, *179*, 103–116.

Garnier, E., Cordonnier, P., Guillerm, J.-L., & Sonié, L. (1997). Specific leaf area and leaf nitrogen concentration in annual and perennial grass species growing in mediterranean old-fields. *Oecologia*, *111*(4), 490–498.

Gioria, M., Hulme, P. E., Richardson, D. M., & Pyšek, P. (2023). Why are invasive plants successful? *Annual Review of Plant Biology*, *74*, 635–670.

Grime, J. P. (2006). Trait convergence and trait divergence in herbaceous plant communities: Mechanisms and consequences. *Journal of Vegetation Science*, *17*, 255–260.

Gross, N., Borger, L., Duncan, R. P., & Hulme, P. E. (2013). Functional differences between alien and native species: Do biotic interactions determine the functional structure of highly invaded grasslands? *Functional Ecology*, *27*, 1262–1272.

Haider, S., Kueffer, C., Bruelheide, H., Seipel, T., Alexander, J. M., Rew, L. J., Arévalo, J. R., Cavieres, L. A., McDougall, K. L., Milbau, A., Naylor, B. J., Speziale, K., & Pauchard, A. (2018). Mountain roads and non-native species modify elevational patterns of plant diversity. *Global Ecology and Biogeography*, *27*, 667–678.

Haider, S., Kueffer, C., Edwards, P. J., & Alexander, J. M. (2012). Genetically based differentiation in growth of multiple non-native plant species along a steep environmental gradient. *Oecologia*, *170*(1), 89–99.

Hakim, N., Ahmad, M., Rathee, S., Sharma, P., Kaur, S., Batish, D. R., & Singh, H. P. (2023). Invasive *Cirsium arvense* displays different resource-use strategies along local habitat heterogeneity in the trans-Himalayan region of Ladakh. *Environmental Monitoring and Assessment*, *195*, 730.

Henn, J. J., Yelenik, S., & Damschen, E. I. (2019). Environmental gradients influence differences in leaf functional traits between native and non-native plants. *Oecologia*, *191*, 397–409.

Hernández-Fuentes, C., Bravo, L. A., & Cavieres, L. A. (2015). Photosynthetic responses and photoprotection strategies of *Phacelia secunda* plants exposed to experimental warming at different elevations in the central Chilean Andes. *Alpine Botany*, *125*, 87–99.

Jin, Y., Liao, M., Hou, Y., Wang, H., Xia, H., Xia, J., Wu, K., Zhou, B., Li, K., & Ni, J. (2024). Spatial patterns and variations in leaf traits of alpine plants on the interior Tibetan Plateau. *Global Ecology and Conservation*, *53*, e03037.

Jin, Y., & Qian, H. (2019). V.PhyloMaker: An R package that can generate very large phylogenies for vascular plants. *Ecography*, *42*, 1353–1359.

Ke, X., Kang, H., & Tang, Y. (2022). Reduction in leaf size at higher altitudes across 39 broad-leaved herbaceous species on the northeastern Qinghai-Tibetan Plateau. *Journal of Plant Ecology*, *15*, 1227–1240.

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*(11), 1463–1464.

Körner, C. (2007). The use of 'altitude' in ecological research. *Trends in Ecology & Evolution*, *22*(11), 569–574.

Körner, C. (2021). *Alpine plant life: Functional plant ecology of High Mountain ecosystems* (3rd ed.). Springer.

Körner, C., Bannister, P., & Mark, A. F. (1986). Altitudinal variation in stomatal conductance, nitrogen content and leaf anatomy in different plant life forms in New Zealand. *Oecologia*, *69*, 577–588.

Kühn, P., Ratier Backes, A., Römermann, C., Bruelheide, H., & Haider, S. (2021). Contrasting patterns of intraspecific trait variability in native and non-native plant species along an elevational gradient on Tenerife, Canary Islands. *Annals of Botany*, *127*, 565–576.

Lambdon, P. W., Lloret, F., & Hulme, P. E. (2008). Do alien plants on Mediterranean islands tend to invade different niches from native species? *Biological Invasions*, *10*, 703–716.

Le Roux, J. (2021). *The evolutionary ecology of invasive species* (1st ed.). Academic Press.

Leishman, M. R., Cooke, J., & Richardson, D. M. (2014). Evidence for shifts to faster growth strategies in the new ranges of invasive alien plants. *Journal of Ecology*, *102*(6), 1451–1461.

Leishman, M. R., Haslehurst, T., Ares, A., & Baruch, Z. (2007). Leaf trait relationships of native and invasive plants: Community- and global-scale comparisons. *New Phytologist*, *176*, 635–643.

Lembrechts, J. J., Pauchard, A., Lenoir, J., Nuñez, M. A., Geron, C., Ven, A., Bravo-Monasterio, P., Teneb, E., Nijs, I., & Milbau, A. (2016). Disturbance is the key to plant invasions in cold environments. *Proceedings of the National Academy of Sciences of the United States of America*, *113*(49), 14061–14066.

Lenth, R. (2022). *emmeans: Estimated marginal means, aka least-squares means*. R package Version 1.8.1-1. https://CRAN.R-project.org/package=emmeans

Lo Gullo, M. A., & Salleo, S. (1988). Different strategies of drought resistance in three Mediterranean sclerophyllous trees growing in the same environmental conditions. *The New Phytologist*, *108*(3), 267–276.

Loiola, P. P., de Bello, F., Chytrý, M., Götzenberger, L., Pérez Carmona, C., Pyšek, P., & Lososová, Z. (2018). Invaders among locals: Alien species decrease phylogenetic and functional diversity while increasing dissimilarity among native community members. *Journal of Ecology*, *106*, 2230–2241.

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. *Journal of Vegetation Science*, *29*, 245–254.

Marini, L., Battisti, A., Bona, E., Federici, G., Martini, F., Pautasso, M., & Hulme, P. E. (2012). Alien and native plant life-forms respond differently to human and climate pressures. *Global Ecology and Biogeography*, *21*, 534–544.

McDougall, K. L., Alexander, J. M., Haider, S., Pauchard, A., Walsh, N. G., & Kueffer, C. (2011). Alien flora of mountains: Global comparisons for the development of local preventive measures against plant invasions. *Diversity and Distributions*, *17*, 103–111.

Naeem, S., Knops, J. M. H., Tilman, D., Howe, K. M., Kennedy, T., & Gale, S. (2000). Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. *Oikos*, *91*, 97–108.

Ordonez, A. (2014). Functional and phylogenetic similarity of alien plants to co-occurring natives. *Ecology*, *95*(5), 1191–1202.

Ordonez, A., Wright, I. J., & Olff, H. (2010). Functional differences between native and alien species: A global-scale comparison. *Functional Ecology*, *24*, 1353–1361.

Pagel, M. (1994). Detecting correlated evolution on phylogenies: A general method for the comparative analysis of discrete characters. *Proceedings of the Royal Society B: Biological Sciences*, *255*, 37–45.

Pauchard, A., Kueffer, C., Dietz, H., Daehler, C. C., Alexander, J., Edwards, P. J., Arévalo, J. R., Cavieres, L. A., Guisan, A., Haider, S., Jakobs, G., McDougall, K., Millar, C., Naylor, B. J., Parks, C. G., Rew, L. J., & Seipel, T. (2009). Ain't no mountain high enough: Plant invasions reaching new elevations. *Frontiers in Ecology and the Environment*, *7*(9), 479–486.

Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M. S., Cornwell, W. K., Craine, J. M., Gurvich, D. E., Urcelay, C., Veneklaas, E. J., Reich, P. B., Poorter, L., Wright, I. J., Ray, P., Enrico, L., Pausas, J. G., de Vos, A. C., … Cornelissen, J. H. C. (2016). New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, *64*, 715–716.

Pérez-Ramos, I. M., Roumet, C., Cruz, P., Blanchard, A., Autran, P., & Garnier, E. (2012). Evidence for a 'plant community economics spectrum' driven by nutrient and water limitations in a Mediterranean rangeland of southern France. *Journal of Ecology*, *100*, 1315–1327.

Petruzzellis, F., Tordoni, E., Tomasella, M., Savi, T., Tonet, V., Palandrani, C., Castello, M., Nardini, A., & Bacaro, G. (2021). Functional differentiation of invasive and native plants along a leaf efficiency/safety trade-off. *Environmental and Experimental Botany*, *188*, 104518.

Pinto-Ledezma, J. N., Villalobos, F., Reich, P. B., Catford, J. A., Larkin, D. J., & CavenderBares, J. (2020). Testing Darwin's naturalization conundrum based on taxonomic, phylogenetic, and functional dimensions of vascular plants. *Ecological Monographs*, *90*(4), e01420.

Qian, H., & Sandel, B. (2017). Phylogenetic relatedness of native and exotic plants along climate gradients in California, USA. *Diversity and Distributions*, *23*, 1323–1333.

R Core Team (2022). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.r-project.org/

Rathee, S., Ahmad, M., Sharma, P., Singh, H. P., Batish, D. R., Kaur, S., Kaur, A., Yadav, S. S., & Kohli, R. K. (2021). Biomass allocation and phenotypic plasticity are key elements of successful invasion of *Parthenium hysterophorus* at high elevation. *Environmental and Experimental Botany*, *184*, 104392.

Reich, P. B. (2014). The world-wide 'fast–slow' plant economics spectrum: A traits manifesto. *Journal of Ecology*, *102*, 275–301.

Revell, L. J. (2012). Phytools: An R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, *3*, 217–223.

Reyes-Bahamonde, C., Piper, F. I., & Cavieres, L. A. (2022). Elevational variation of the seasonal dynamic of carbohydrate reserves in an alpine plant of Mediterranean mountains. *Alpine Botany*, *132*, 315–327.

Richardson, D. M. (2011). Invasion science: The roads travelled and the roads ahead. In D. M. Richardson (Ed.), *Fifty years of invasion ecology: The legacy of Charles Elton* (pp. 396–407). Wiley-Blackwell.

Richardson, D. M., & Rejmánek, M. (2004). Conifers as invasive aliens: A global survey and predictive framework. *Diversity and Distributions*, *10*, 321–331.

Ricotta, C., Godefroid, S., & Rocchini, D. (2010). Invasiveness of alien plants in Brussels is related to their phylogenetic similarity to native species. *Diversity and Distributions*, *16*, 655–662.

Santibáñez, F., & Uribe, J. M. (1990). *Atlas agroclimático de Chile: regiones V y Metropolitana*. Fondo Nacional de Desarrollo Científico y Tecnológico.

Schöb, C., Armas, C., Guler, M., Prieto, I., & Pugnaire, F. I. (2013). Variability in functional traits mediates plant interactions along stress gradients. *Journal of Ecology*, *101*, 753–762.

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. *Ecology and Evolution*, *14*, e10888.

Schumacher, E., Kueffer, C., Tobler, M., Gmür, V., Edwards, P. J., & Dietz, H. (2008). Influence of drought and shade on seedling growth of native and invasive trees in the Seychelles. *Biotropica*, *40*(5), 543–549.

Seguí, J., Lázaro, A., Traveset, A., Salgado-Luarte, C., & Gianoli, E. (2018). Phenotypic and reproductive responses of an Andean violet to environmental variation across an elevational gradient. *Alpine Botany*, *128*, 59–69.

Sierra-Almeida, A., Cavieres, L. A., & Bravo, L. A. (2009). Freezing resistance varies within the growing season and with elevation in high-Andean species of central Chile. *New Phytologist*, *182*(2), 461–469.

Strauss, S. Y., Webb, C. O., & Salamin, N. (2006). Exotic taxa less related to native species are more invasive. *Proceedings of the National Academy of Sciences of the United States of America*, *103*, 5841–5845.

Tecco, P. A., Díaz, S., Cabido, M., & Urcelay, C. (2010). Functional traits of alien plants across contrasting climatic and land-use regimes: Do aliens join the locals or try harder than them? *Journal of Ecology*, *98*(1), 17–27.

Tellier, S., Marticorena, A., & Niemeyer, H. (2011). *Flora Andina de Santiago. Guía para la identificación de las especies de las cuencas del Maipo y del Mapocho*. Universidad de Chile.

Thuiller, W., Gallien, L., Boulangeat, I., de Bello, F., Münkemüller, T., Roquet, C., & Lavergne, S. (2010). Resolving Darwin's naturalization conundrum: A quest for evidence. *Diversity and Distributions*, *16*, 461–475.

Valiente-Banuet, A., & Verdú, M. (2007). Facilitation can increase the phylogenetic diversity of plant communities. *Ecology Letters*, *10*, 1029–1036.

Verdú, M., Gómez-Aparicio, L., & Valiente-Banuet, A. (2012). Phylogenetic relatedness as a tool in restoration ecology: A meta-analysis. *Proceedings of the Royal Society B*, *279*, 1761–1767.

Wang, G., Zhang, X., Yannelli, F., Li, J.-J., Shi, S., Zhang, T., Bie, X., Chen, X., Peng, P.-H., & Jiang, L. (2024). The impact of species phylogenetic relatedness on invasion varies distinctly along resource versus non-resource environmental gradients. *Journal of Applied Ecology*, *61*, 869–883.

Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J. H. C., Diemer, M., Flexas, J., Garnier, E., Groom, P. K., Gulias, J., Hikosaka, K., Lamont, B. B., Lee, T., Lee, W., Lusk, C., … Villar, R. (2004). The worldwide leaf economics spectrum. *Nature*, *428*, 821–827.

Yang, M., Lu, Z., Fan, Z., Liu, X., Hens, L., De Wulf, R., & Ou, X. (2018). Distribution of non-native plant species along elevation gradients in a protected area in the eastern Himalayas, China. *Alpine Botany*, *128*, 169–178.

Yannelli, F. A., Koch, C., Jeschke, J. M., & Kollmann, J. (2017). Limiting similarity and Darwin's naturalization hypothesis: Understanding the drivers of biotic resistance against invasive plant species. *Oecologia*, *183*, 775–784.

Zhang, L., Mi, X., & Shao, H. (2016). Phylogenetic relatedness influences plant interspecific interactions across stress levels in coastal ecosystems: A meta-analysis. *Estuaries and Coasts*, *39*, 1669–1678.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Map showing the location of study sites along an elevational gradient in the Andes of central Chile.

Figure S2. Phylogenetic tree of angiosperm species occurring in the central Chilean Andes.

Figure S3. Number of annual and perennial species per biogeographic origin (native or non-native) along an elevational gradient.

Figure S4. Pairwise phylogenetic distances from non-native species to native ones along an elevational gradient.

Table S1. A list of the plant species recorded at each elevation.

Table S2. GLM results. Mean phylogenetic (MPD) and functional (MFD) distances between native and non-native plant species were modelled as a function of elevation.

Table S3. Multiple comparisons for five functional traits of native and non-native species across different elevations.

Table S4. Testing for phylogenetic signal in leaf morphological traits and chlorophyll content.

How to cite this article: Anic, V., Mihoč, M., Valencia, G., Reyes-Bahamonde, C., Bravo, L. A., Sáez, P. L., Pauchard, A., & Cavieres, L. A. (2025). Functional and phylogenetic similarity between native and non-native plant species along an elevational gradient in the central Chilean Andes: No evidence for the preadaptation hypothesis. *Journal of Ecology*, *00*, 1–14. https://doi.org/10.1111/1365-2745.70089