

Taxonomic distinctness of climbing plants and epiphytes in central-Chilean forests: an alternative diversity measure from unequal species lists

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Protected wild areas aim to conserve biodiversity. However, a lack of monitoring limits the availability of biological information needed to achieve this goal. This study used taxonomic distinctness (Δ^+), its variance (Λ^+), and a combined metric of both measures as alternative methods to monitor the diversity of climbing plants and vascular epiphytes in the absence of standardized data over time and space. The study was conducted in five forested small protected areas within the biodiversity hotspot of central Chile. The method involved updating the species inventory and comparing it with those from previous studies. The results showed that epiphytes followed a general pattern of increasing diversity towards the south along the latitudinal gradient (Δ^+ between 54.95 and 73.3), while climbers remained more stable (Δ^+ between 70.33 and 72.33). The combined analysis of both indices (Δ^+ and Λ^+) suggested that both climbers and epiphytes gained taxonomic diversity over time at most sites ($p < 0.05$). Sites that did not follow this general pattern may reflect differences in sampling design between the original and current inventories, which may have influenced the results. This observation requires further investigation as anthropogenic pressures may explain these variations. Future research should focus on long-term monitoring of the taxonomic distinctness of both assemblages to assess their responses to environmental disturbance and climate change, thereby providing a basis for developing more effective conservation strategies.

Keywords: Biodiversity Hotspot, Ecotone, Species Composition, Vascular Plants

Introduction

One of the primary objectives of protected wild areas is the conservation of biodiversity, particularly in the context of global climate change and increasing demand for ecosystem goods and services. This demand is placing growing pressure on these areas and the species inhabiting them (Pereira & Cooper 2006). Achieving

this objective necessitates access to information that enables the study of changes in biodiversity (e.g., species composition or richness) across time and space, typically through inventories or monitoring programs. However, logistical constraints such as accessibility, funding, and time, often hinder comprehensive species sampling within a given area. In this context, vascular indicator plants represent a practical starting point for long-term monitoring programs (Domínguez et al. 2012). Changes in the distribution of these species can provide insights into local climate variations or the effects of habitat modification, and their diversity is a reliable predictor of the diversity of other taxa (Pereira & Cooper 2006).

Despite the potential benefits offered by indicator species, the implementation of inventories or other systematic sampling strategies in protected areas remains an unresolved issue in most Latin American countries and globally. This is mainly because such activities are resource-intensive and must be linked to national policies. The limited availability of data for species conservation is a recognized problem (Lindenmayer et al. 2010). In the absence of a formal data collection strategy, using existing information from previous studies becomes a viable alternative. This secondary

information, such as floristic catalogs, is often derived from sources with varying objectives, methods, and times of collection, and generally only provides occurrence data (presence-absence).

Although citizen science initiatives currently offer promising alternatives for advancing biodiversity studies, large-scale biodiversity databases (e.g., GBIF – <https://www.gbif.org>) still present significant challenges, including inconsistencies in taxonomic resolution, spatial biases, and variable data quality depending on the original sources (Zizka et al. 2019). These issues can limit the comparability of heterogeneous data across time and space (Domínguez et al. 2012). Nevertheless, certain analytical approaches enable the effective utilization of these datasets for preliminary assessments, such as determining the conservation status of individual species or species groups. Such approaches include taxonomic distinctness indices (Clarke & Warwick 2001), species distribution modeling (Pena et al. 2014), and gap analysis (Ahmadi et al. 2020).

A significant challenge in biodiversity assessments is the use of non-standardized or incomplete datasets (Domínguez et al. 2012). Basic diversity metrics such as species richness and similarity indices can be heavily influenced by sampling intensity

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and completeness, which frequently vary between datasets and are often not explicitly reported. Consequently, indices based solely on species richness or composition might not reliably detect subtle yet ecologically relevant changes. Furthermore, assemblage composition may shift substantially due to long-term environmental changes or disturbances, further complicating comparisons. Although strategies such as rarefaction curves (Chao et al. 2014) and species richness estimators (Chao 1984) can partially address these sampling biases, these methods remain sensitive to temporal and spatial variability in sampling intensity. Despite these limitations, species inventories, floristic catalogs, and other biodiversity datasets contain valuable biological information that reflects the taxonomic relationships among species. In this context, taxonomic distinctness offers a valuable complementary approach (Clarke & Warwick 2001).

Taxonomic distinctness refers to the degree to which species in a community are evolutionarily or taxonomically related, encompassing both the ecological roles and shared evolutionary histories that shape community structure. In this context, taxonomic distinctness indices (Δ^+ and Λ^+) offer a robust way to measure and compare how closely or distantly related species are, based on the hierarchical distance between taxa at higher levels (e.g., genus, family, order). Specifically, Δ^+ captures the average taxonomic distance among species, whereas Λ^+ measures the variance in those distances (Clarke & Warwick 1998, 2001, Ellingsen et al. 2005). By emphasizing taxonomic relationships rather than simple species counts, these indices offer a more nuanced measure of biodiversity. A major advantage of taxonomic distinctness indices is their independence from sampling effort, enabling reliable comparisons across different studies and conditions, even when species richness or sampling methodologies vary (Clarke & Warwick 1998). They also exhibit high sensitivity to environmental stress, responding clearly to disturbances such as habitat degradation or pollution and thus serving as valuable tools for ecosystem health monitoring. Moreover, these indices explicitly measure changes in taxonomic relationships at hierarchical levels beyond the species rank, recognizing that an assemblage spanning a broader range of higher-level categories (e.g., several families or orders) reflects greater evolutionary diversity than one concentrated within a few genera or families. Owing to their robustness as ecological indicators, taxonomic distinctness indices remain relatively unaffected by habitat differences and can be applied across a broad range of ecosystems (Ellingsen et al. 2005). By capturing both community-wide patterns and deeper ecological and evolutionary processes, Δ^+ and Λ^+ provide insights into biodiversity that transcend mere species counts.

These taxonomic distinctness indices typically rely on a master species list, a carefully constructed reference that accurately reflects the regional taxonomic structure (Clarke & Warwick 1998, 2001). When the master list and the sampling methods are well-aligned, Δ^+ and Λ^+ can determine whether particular subsets of species (sites, time periods) adequately mirror the taxonomic composition of the broader region. Such relative independence from sampling size and effort is especially helpful for historical comparisons or studies with uneven or uncontrolled sampling. It can also help identify impacted sites or areas of exceptional taxonomic richness (Ellingsen et al. 2005). This approach can be applied spatially (e.g., comparing local against regional assemblages) and temporally (e.g., spanning decades or centuries), making it invaluable in scenarios where standardizing sample sizes proves impractical. However, the accuracy of these indices depends on maintaining a sufficiently well-resolved taxonomic hierarchy and comparable sampling protocols (Clarke & Warwick 1998).

Although taxonomic distinctness indices have been widely applied in marine and freshwater environments (Bevilacqua et al. 2011, Jiang et al. 2020), their use in terrestrial ecosystems remains less common (Silva & Batalha 2006). The aim of this study is to contribute to the application of these indices in forest ecosystems by analysing species inventories in five small protected wild areas distributed along the coast of central Chile, a region recognised as a global biodiversity hotspot (Myers et al. 2000). The study areas include Los Riles National Reserve (45 ha), Los Queules National Reserve (146 ha), Contulmo Natural Monument (82 ha), Rucamanque Estate (330 ha), and Cerro Nielol Natural Monument (89 ha). These units are located in a climatic and vegetation transition zone, where sclerophyllous vegetation from the north and temperate forest from the south converge (Luebert & Plissock 2006). The selection of these areas was based on the availability of historical inventory data, which provides the opportunity to compare changes in species diversity over time and detect signals of ecosystem or climatic shifts (Domínguez et al. 2012).

The literature suggests that climbing plants and vascular epiphytes, such as filmy ferns, may serve as indicator species for habitat structure changes and ecosystem disturbance levels in forests. These plants are highly dependent on forest trees for their survival and display differentiated responses to environmental gradients (Zotz 2016, Pincheira-Ulbrich et al. 2018). For example, more humid conditions in the lower section of tree trunks create more favorable microhabitats for epiphytic ferns (Hymenophyllaceae – Saldaña et al. 2014), while climbers prefer clearings or sites with greater direct solar radiation (Carrasco-Urra & Gianoli 2009).

The principal aim of this study is to assess temporal changes in the taxonomic distinctness of assemblages composed of forest climbing plants and epiphytes. To achieve this, the species lists from each wildlife reserve were compared against a master species list compiled from historical and current inventories. Taxonomic distinctness was evaluated using both average taxonomic distinctness (Δ^+) and its variance (Λ^+). These two indices were first analyzed independently and then combined, as their simultaneous use (Δ^+ and Λ^+) offers greater sensitivity for detecting subtle shifts in taxonomic structure, particularly concerning species distribution and relatedness within assemblages.

The starting hypothesis is that the taxonomic diversity of climbing plants has increased over time, whereas the diversity of epiphytes has decreased. This expectation is based on the premise that epiphytes, lacking effective mechanisms for moisture regulation, are primarily restricted to stable, humid microhabitats (Dubuisson et al. 2009). Temporal changes in diversity patterns are thus considered a response to the increasing influence of the Mediterranean climate on forest structure and composition, potentially exacerbated by anthropogenic pressures, such as the growing number of visitors in protected areas (Subsecretaría de Turismo 2022). Such pressure could fragment habitats, amplify edge effects, and limit suitable colonization opportunities for epiphytes, while simultaneously creating favorable conditions for climbing plants (Pincheira-Ulbrich et al. 2018). Thus, differences in taxonomic composition between epiphyte and climber assemblages may reflect underlying environmental pressures, providing insights to support efforts aimed at updating species inventories and improving management practices in protected wild areas.

Materials and methods

Description of the study area

The study area is situated within the Mediterranean-temperate phytogeographic interaction zone of central Chile, encompassing five protected wild areas: Los Riles National Reserve (45 ha), Los Queules National Reserve (146 ha), Contulmo Natural Monument (82 ha), Rucamanque Estate (330 ha), and Cerro Nielol Natural Monument (89 ha). These sites, located within a highly fragmented landscape dominated by *Pinus radiata* D. Don plantations, form part of the coastal range (Fig. 1) and are recognized as one of the world's biodiversity hotspots (Myers et al. 2000).

The geographic coordinates of the study area range from 35° 49' 59.38" S, 72° 29' 48.76" W at Los Riles National Reserve to 38° 43' 18.86" S, 72° 35' 12.35" W at Cerro Nielol Natural Monument. The climate shifts from Mediterranean with oceanic influence in the north to temperate with Mediterranean influence in the south. An-

nual rainfall varies from 1086 mm at Los Riles, with an average temperature of 10.8 °C, to 1240 mm at Cerro Ñielol, where the average temperature is 10.9 °C (Luebert & Plissock 2006).

The predominant vegetation in the region reflects the climatic transition: Mediterranean deciduous forests in the north, with species such as *Nothofagus glauca* (Phil.) Krasser and *Persea lingue* (Ruiz & Pav.) Nees, and temperate deciduous forests in the south, dominated by *Nothofagus obliqua* (Mirb.) Oerst. and *Laurelia sempervirens* (Ruiz & Pav.) Tul. Common species across the region include *Nothofagus* spp., and *Cryptocarya alba* (Molina) Looser. Climbers and epiphytes are also widespread throughout these areas (Luebert & Plissock 2006).

Sampling design and data collection

A non-random sampling design was employed to capture greater microhabitat variation and maximize the detection of rare species (Diekmann et al. 2007). Trails and ravines were used as natural transects (Brower et al. 1990), along which all vascular plant species were identified and recorded. Within these transects, circular plots (3 m in diameter, 7.06 m²) were established, applying an intensive survey approach to ensure a thorough assessment of species composition (Pincheira-Ulbrich et al. 2018).

Within each plot, all epiphytes and climbing plants were recorded from the ground up to a height of 2.3 meters on tree trunks with a diameter at breast height (DBH) ≥ 3 cm. Additionally, climbing plants at juvenile stages, including those growing on the ground, and individuals colonizing fallen logs were documented.

Sampling was conducted between 2018 and 2023, with a total of 100 plots established. Surveys were carried out in Cerro Ñielol in 2018 (25 plots), Contulmo in 2020 (15 plots), and in Los Queules (17 plots), Los Riles (21 plots), and Rucamanque (22 plots) between 2022 and 2023.

Epiphytes were identified following the criteria established by Larsen et al. (2013), while the identification of climbing plants followed the guidelines provided by Marti-corena et al. (2010). Some specimens were also identified with the assistance of the herbarium at the University of Concepción (CONC), Chile.

Historical inventories

The bibliographic sources for the floristic species lists were drawn from five key studies, each employing different methodologies that combined exhaustive vegetation censuses, phytosociological inventories, systematic sampling, and herbarium records.

For Cerro Ñielol Natural Monument, Hauenstein et al. (1988) conducted vegetation censuses between 1980 and 1984, complemented by phytosociological inventories using Braun-Blanquet's approach to de-

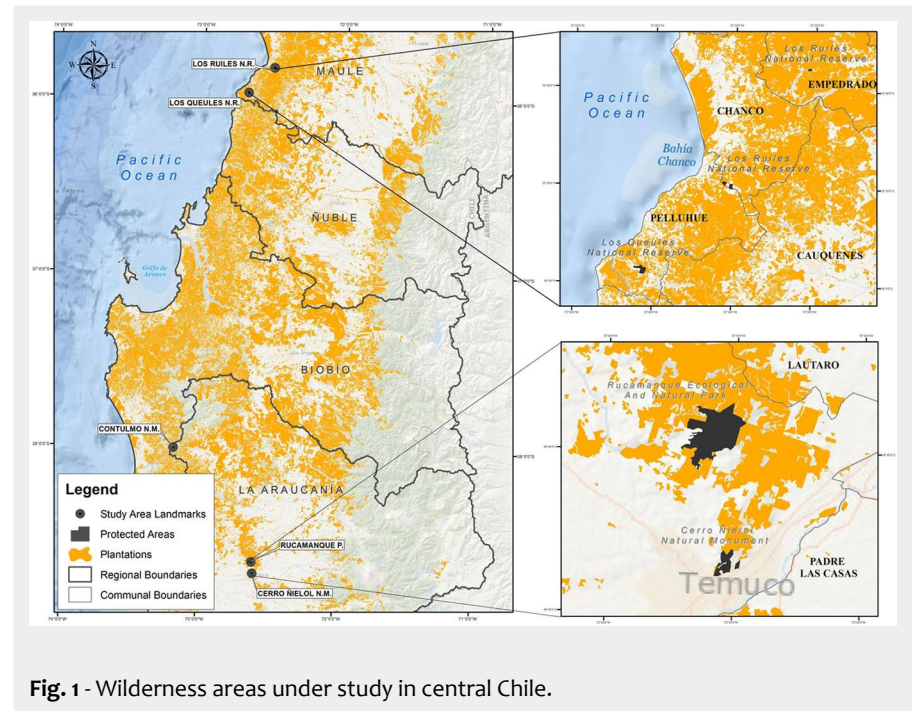


Fig. 1 - Wilderness areas under study in central Chile.

scribe species composition and classify vegetation associations. Similarly, for Rucamanque Estate, Ramírez et al. (1989) conducted censuses using a phytosociological framework.

In Contulmo Natural Monument, Baeza et al. (1999) compiled the most comprehensive floristic catalogue based on botanical field explorations, complemented by herbarium records to ensure taxonomic accuracy. Similarly, for Los Queules and Los Riles National Reserves, Arroyo et al. (2005) conducted botanical surveys across diverse habitats in 1999 and 2000, integrating these data with herbarium records from national and international collections.

To analyze the taxonomic distinctness of climber and vascular epiphyte assemblages, the taxonomic tree structure was defined using six hierarchical levels of the standard Linnaean classification: species, genus, family, order, class, and phylum. The classification framework was derived from the "Catalogue of Life" (Bánki et al. 2024). Each protected wild area was considered a sample representing the taxonomic diversity of the phylogeographic region at two distinct time points: (i) historical records compiled from the aforementioned bibliographic sources, and (ii) contemporary field surveys conducted as part of this study, allowing for a comparative analysis of species composition. Historical inventories are identified by an abbreviation followed by a two-digit code representing the year of the survey (e.g., MNC83 = 1983, RQE89 = 1989). In contrast, current inventories use the same abbreviation without the numerical suffix (e.g., MNC, RQE, CTM, LQLES, LRLLES).

Analysis of taxonomic structure

The taxonomic structure of the samples (i.e., the wild areas) was quantified using

taxonomic distinctness indices: average taxonomic distinctness (Δ^+ , eqn. 1) and its variance (Λ^+ , eqn. 2), following the methods of Clarke & Gorley (2015). This analysis was performed separately for vascular epiphyte and climbing plant assemblages, as their distinct biological traits may influence habitat structure and responses to climatic conditions (Pincheira-Ulbrich et al. 2018):

$$\Delta^+ = \frac{\sum_{i < j} \omega_{ij}}{S(S-1)/2} \quad (1)$$

$$\Lambda^+ = \frac{\sum_{i < j} (\omega_{ij} - \Delta^+)^2}{S(S-1)/2} \quad (2)$$

The average taxonomic distinctness (Δ^+) for an observed number of species (S) in a sample represents the weighted average of the taxonomic distances between all species pairs, measured within the taxonomic hierarchy. These distances, denoted as ω_{ij} , correspond to the number of hierarchical levels separating each species pair (i, j). Each level in the taxonomic classification contributes a predefined weight to the total distance, following the methodology of Clarke & Warwick (2001). The maximum possible distance assigned to species from different phyla is set to 100 and divided into six equal steps across the taxonomic hierarchy. Consequently, species within the same genus have a taxonomic distance of 16.6, those at the family level are assigned a weight of 33.3, and species from different phyla retain the maximum distance of 100. The Δ^+ index is calculated by summing all taxonomic distances between unique species pairs ($\sum_{i < j} \omega_{ij}$), normalized by the total number of species pairs [$S(S-1)/2$].

Since Δ^+ represents the average taxonomic distance among species in a community, the addition of new species does not necessarily lead to greater taxonomic dis-

tinctness. When the newly added species are taxonomically closely related (e.g., within the same genus), they introduce comparisons with lower taxonomic distances, reducing the mean taxonomic distance and thereby decreasing Δ^+ . Conversely, if the new species belong to more distantly related taxa, Δ^+ may increase or remain stable depending on their placement within the taxonomic hierarchy.

While Δ^+ quantifies the average taxonomic distance or branch length, it does not provide information about the overall shape of the taxonomic tree. To address this, the variance in taxonomic distinctness (Λ^+) is calculated, measuring the dispersion of taxonomic distances relative to the mean Δ^+ value. This calculation involves summing the squared deviations of each taxonomic distance from Δ^+ [$\sum_{i \in j} (\omega_{ij} - \Delta^+)^2$]. Λ^+ helps distinguish assemblages with different branching distributions, such as those with high species richness within certain genera or higher hierarchical taxa represented by only a single species (Clarke & Warwick 2001).

The hypothesis tested was that the samples (i.e., the wild areas), each comprising n species, represent sub-lists randomly drawn from a master species list encompassing all taxa present across the wild areas, and thus do not differ significantly in their taxonomic structure from the expectation under a null model of random species assembly based on this master list.

This analysis assumes that historical inventories were sufficiently intensive to capture most of the species present across all study sites, ensuring that the master list is representative of the regional taxonomic structure defined by the sampled sites. Under these conditions, Taxonomic Distinctness (Δ^+) is theoretically independent of sample size and survey effort (Clarke & Warwick 1998). Consequently, any observed differences in Δ^+ are expected to reflect genuine variations in taxonomic structure across sites rather than artifacts of sampling effort.

To test this hypothesis, sub-lists of five species were randomly extracted, with their size progressively increased by a factor of 1.2 (the default setting in PRIMER software, e.g., 4, 4.8 $\approx$ 5, 6.9 $\approx$ 7), up to the maximum number of species recorded at the richest site. Each sub-list was then randomly permuted 10,000 times, generating new taxonomic distinctness indices for these permuted subsets, based on the construction of new taxonomic trees. This process built the probability distribution under the null hypothesis, establishing 95% confidence intervals for both the average (Δ^+) and variance (Λ^+) of taxonomic distinctness (Clarke & Gorley 2015).

It is important to note that this method does not conduct direct statistical comparisons between sites. Instead, it assesses deviations from a null expectation derived from the master species list.

Following the same rationale, the simultaneous relationship between both indices (Δ^+ , Λ^+) was examined using an ellipse plot, one for each sublist size. Under the null hypothesis – which assumes that observed taxonomic distinctness values result from a random assembly model based on the master species list – each confidence ellipse serves as a reference to evaluate two key aspects: (i) whether communities conform to the overall taxonomic structure of the master list, as indicated by their position inside or outside the central 95% confidence ellipse, and (ii) whether species sublists of a given size exhibit the expected taxonomic distinctness. The null distribution for each sublist size was estimated through 10,000 simulations of species sublists, progressively increasing in size at fixed intervals.

To account for differences in species richness across sites, sublist sizes were adjusted separately for each plant group. For epiphytes, sublists were constructed in 5-species intervals (5, 10, 15, and 20), with each interval generating a distinct confidence ellipse, where 20 represents the total species richness in the master list. For climbing plants, sublists ranged from 15 to 35 species, following the same approach, with 35 representing the total recorded richness. This adjustment ensures that confidence ellipses reflect realistic expectations for each taxonomic group.

This graphical approach enhances the de-

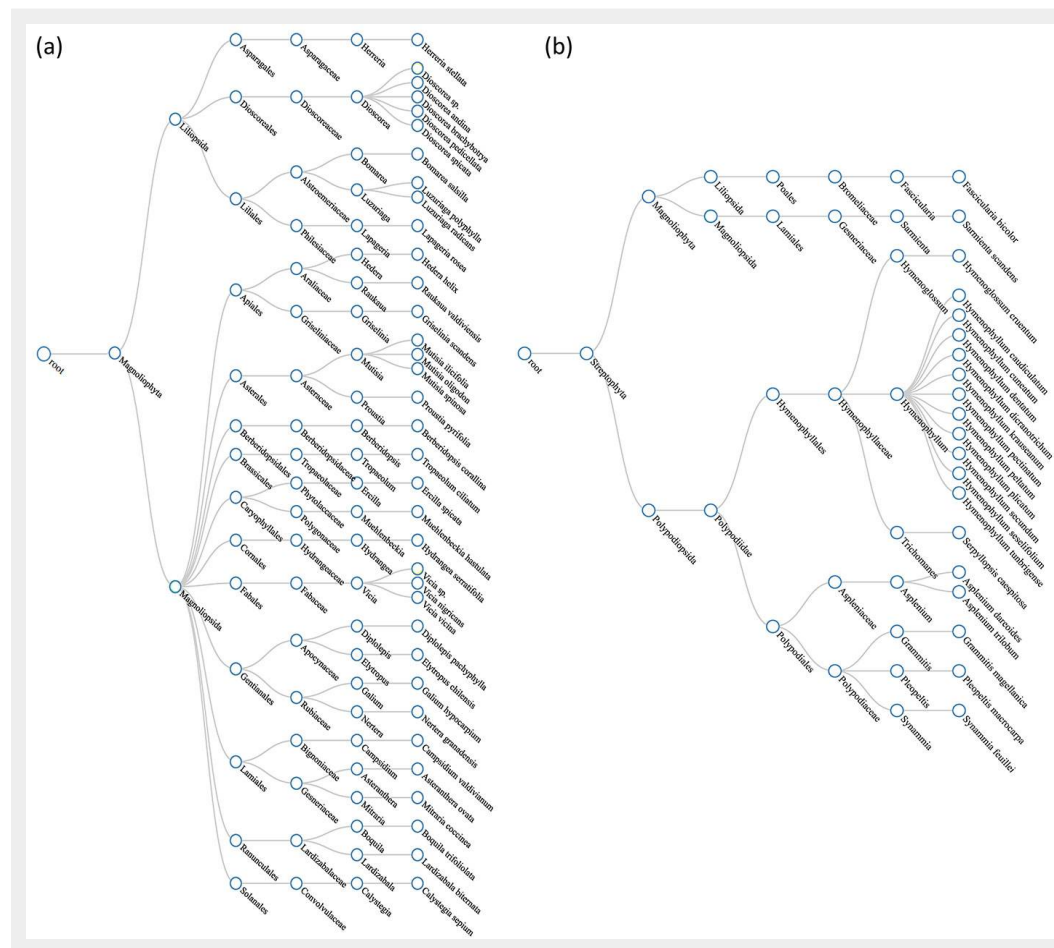


Fig. 2 - Taxonomic structure of the master list for (a) epiphytes and (b) climbing plants.

tection of deviations from the expected taxonomic structure that might not be statistically significant when assessed separately. Notably, when a site falls within a given confidence ellipse, its taxonomic structure aligns with the expected pattern for a community composed of that number of species randomly drawn from the master list (e.g., a site within the 10-species ellipse follows the expected structure for 10 species). Further, when a site falls exactly on the boundary of an ellipse, its taxonomic distinctness matches the expected threshold for that species richness level. Conversely, when two points are located in distinct regions separated by an ellipse, their taxonomic distinctness is considered significantly different ($p < 0.05$ – Clarke & Warwick 2001).

Taxonomic trees were constructed using Taxallnomy (<http://biodados.icb.ufmg.br/taxallnomy/>), a database maintained by the Biodata Laboratory of the Federal University of Minas Gerais, based on NCBI Taxonomy. Species absent from the NCBI taxonomy were manually added by modifying the SVG file generated by Taxallnomy, adapting it to the taxonomy used in this study (see Tab. S2 and Tab. S4 in Supplementary materials). All calculations and the ellipse plottings were performed using the TAXDEST routine in PRIMER v. 7 software (Clarke & Gorley 2015).

Results

Composition and taxonomic structure

The taxonomic structure of climbing plants in the five protected wild areas of central Chile showed higher taxonomic distinctness (Δ^+) than that of epiphytes, as reflected by a greater number of families and genera (Fig. 2). Epiphytes were predominantly ferns, largely from the genus *Hymenophyllum*. Overall, climbing plants displayed a more stable taxonomic composition across sites. In contrast, epiphytes exhibited greater variability, with new species recorded in surveys of this study (see Tab. S3 and Tab. S4 in Supplementary material).

Epiphytes

A total of 20 epiphyte species were documented, distributed across nine genera, five families, and four orders. Species richness per site remained relatively stable between the initial inventories (4–17 species) and the most recent surveys conducted in this study (5–17 species – Tab. S1, Tab. S2). However, site-specific comparisons revealed that Cerro Ñielol (MNC) and Rucamanque (RQE) had the most significant increases, with five additional species recorded compared to previous inventories.

Species such as *Asplenium dareoides* Desv. and *Synammia feuillei* (Bertero) Copel. have been consistently recorded across all sites along the latitudinal gradient. In contrast, species like *Hymenophyllum seselifolium* C. Presl and *Pleopeltis macrocarpa*

Tab. 1 - Comparison of the taxonomic distinctness of vascular epiphyte and climbing plant assemblages in five wild areas relative to the master species list (36 species for climbers, 20 species for epiphytes). Sample codes: Cerro Ñielol Natural Monument (MNC, MNC83), Rucamanque (RQE, RQE89), Contulmo Natural Monument (CTM, CTM99), Los Queules National Reserve (LQLES, LQLES05), Los Ruiles National Reserve (LRLES, LRLES05). Acronyms with numbers (e.g., MNC83, CTM99) refer to historical inventories, while acronyms without numbers (e.g., MNC, CTM) correspond to current inventories conducted in this study. Variables – (Δ^+): average taxonomic distinctness, (Λ^+): variance of taxonomic distances; (S): species richness; (p-value): probability associated with the null hypothesis of no difference between species samples and the master species list, obtained from 10,000 simulations; (na): not applicable.

Group	Samples	S	Taxonomic distinctness			
			Δ^+	p-value	Λ^+	p-value
Epiphytes	MNC	14	54.95	0.836	1181.29	0.087
	MNC83	10	65.93	0.174	1024.14	0.430
	RQE	17	55.15	0.758	966.15	0.607
	RQE89	11	64.24	0.209	973.92	0.704
	CTM	15	58.89	0.188	920.99	0.861
	CTM99	17	57.84	0.007	878.03	0.789
	LQLES	11	62.73	0.282	1090.54	0.298
	LQLES05	7	75.40	0.077	836.48	0.913
	LRLES	5	73.33	0.261	677.78	0.689
	LRLES05	4	55.56	0.985	339.51	0.625
Climbers	Master list	20	53.25	na	929.52	na
	MNC	19	72.22	0.153	172.19	0.988
	MNC83	18	72.33	0.135	134.94	0.409
	RQE	17	70.96	0.881	142.96	0.548
	RQE89	20	71.75	0.411	129.09	0.232
	CTM	18	71.13	0.982	174.32	0.963
	CTM99	20	71.40	0.733	141.31	0.398
	LQLES	19	72.03	0.239	128.83	0.276
	LQLES05	19	72.32	0.089	117.49	0.155
	LRLES	23	71.48	0.486	158.03	0.603
Climbers	LRLES05	16	71.94	0.469	185.11	0.794
	Master list	36	70.90	na	179.61	na

(Bory ex Willd.) Kaulf. were only documented in the initial inventories at Contulmo (CTM).

The most diverse family was Hymenophyllaceae, represented by 13 species. Consequently, the genus *Hymenophyllum* (including 11 species) and the order Hymenophyllales (including 13 species) were the most represented. This family of filmy ferns demonstrated notable variability in species richness along the latitudinal gradient, suggesting that temporal and spatial changes in the taxonomic structure of the study sites were largely driven by changes in the species composition of this family. For instance, five species not observed in the initial inventory were documented at Cerro Ñielol: *Hymenophyllum cuneatum*, *H. dicranotrichum*, *H. pectinatum*, *H. peltatum*, and *H. tunbrigense*.

Climbers

The climber assemblage exhibited greater taxonomic richness than epiphytes, with a total of 36 species recorded across 27

genera, 17 families, and 13 orders (Tab. S3 and Tab. S4 in Supplementary material). Species richness per site ranged from 16 to 20 in the initial inventories and from 17 to 23 in the most recent surveys. The most notable increase was observed at Los Ruiles (LRLES), where the current inventory recorded 23 species, compared to 16 in the previous survey.

Species such as *Bomarea salsilla* (L.) Mirb., *Lapageria rosea* Ruiz & Pav., and *Muehlenbeckia hastulata* (Sm.) I.M. Johnst. have maintained their presence over time at all sites along the latitudinal gradient. In contrast, species like *Boquila trifoliolata* (DC.) Decne. and *Cissus striata* Ruiz & Pav. were recorded only in the current inventories at Los Ruiles and Los Queules, respectively.

The most frequently occurring families were Dioscoreaceae (five species), Asteraceae (four species), and Fabaceae (three species). The most frequently occurring genera were *Dioscorea* (five species), *Mutisia* (three species), and *Vicia* (three species). The most representative orders were Dios-

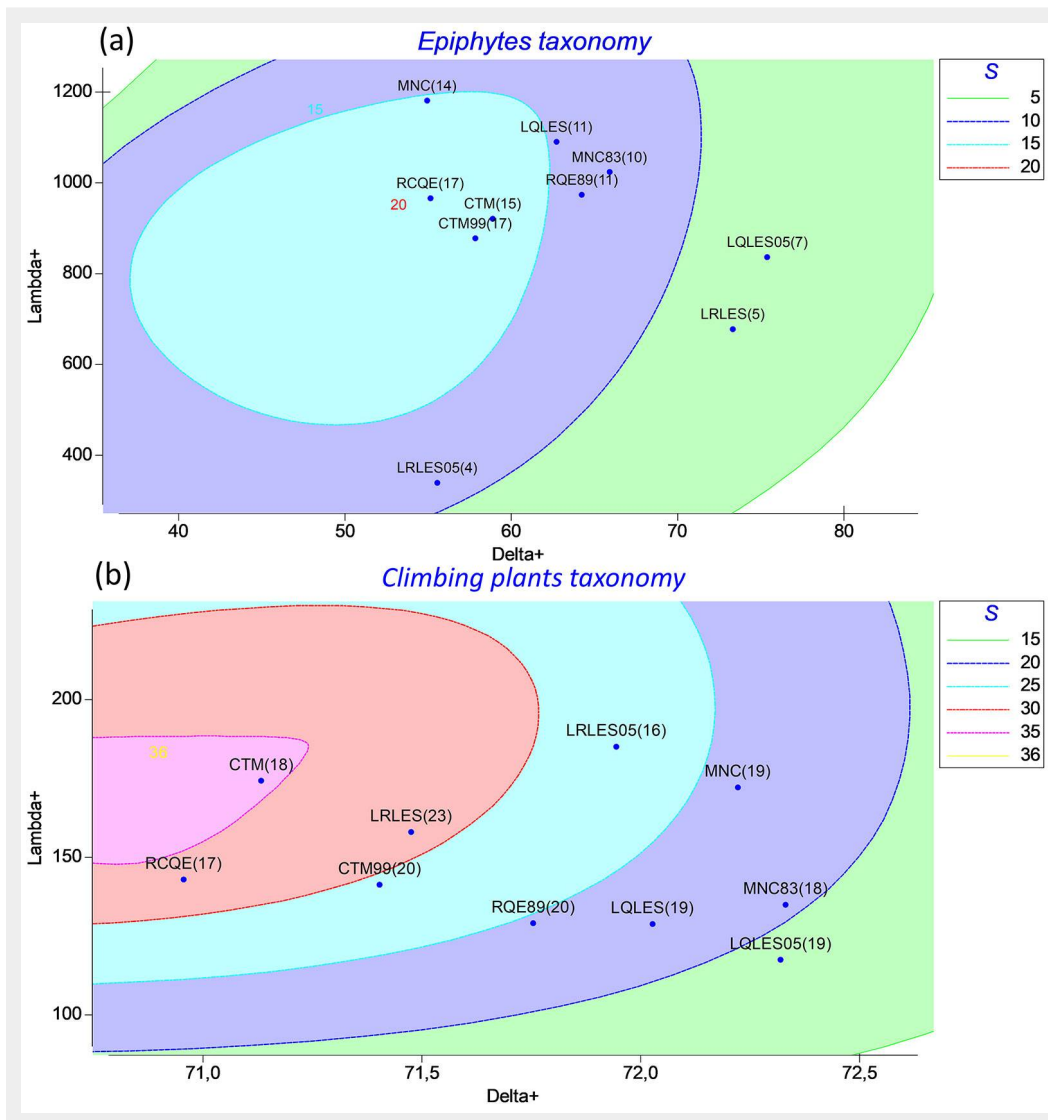


Fig. 3 - Ellipse graph simultaneously relating the taxonomic distinctness (Δ^+ , x-axis) and the variance of taxonomic distinctness (Λ^+ , y-axis) at two points in time. Epiphytes (a) and Climbing plants (b). Species richness (S) is shown in parentheses. Confidence limits for the contours were constructed by randomly extracting sublists (S) of 5 species with 10,000 simulations for 95% confidence. Sample codes: Cerro Ñielol Natural Monument (MNC, MNC83), Rucamanque (RQE, RQE89), Contulmo Natural Monument (CTM, CTM99), Los Queules National Reserve (LQLES, LQLES05), Los Ruiles National Reserve (LRLES, LRLES05).

coreales (five species), Liliales (four species), Gentianales (four species), and Asterales (four species).

Although the overall species composition remained largely stable across sites and between the historical and current inventories, some notable changes were observed. For instance, while the *Dioscoreaceae* family was present in both periods, the representation of its species varied. *Dioscorea auriculata* Poepp. was recorded at most sites, whereas *Dioscorea pedicellata* Phil. exhibited shifts in distribution between historical and current inventories.

Similarly, *Mitraria coccinea* Cav. was absent from the current inventory at Cerro Ñielol, while *Elytropus chilensis* (A. DC.) Müll. Arg. was recorded only in the most recent inventory. These species turnover events introduced some degree of variation in taxonomic structure and family composition.

Taxonomic distinctness

Epiphytes

The average taxonomic distinctness (Δ^+) in the current inventories ranged from 54.95 at Contulmo (CTM) to 73.3 at Los

Ruiles (LRLES), representing the sites with the lowest and highest taxonomic distinctness, respectively. This pattern suggests a northward increase in taxonomic distinctness along the latitudinal gradient, despite a concurrent decrease in species richness. However, in most sites, these variations were not statistically significant when compared to the master species list, which has an expected Δ^+ of 53.25 ($p > 0.05$ – Tab. 1).

At Contulmo, the first inventory (CTM99) exhibited a highly significant difference from the master species list ($\Delta^+ = 57.84$, $p = 0.007$), indicating that its taxonomic distinctness was previously higher than in the current inventory (CTM, $\Delta^+ = 58.89$, $p = 0.188$). This suggests that its taxonomic structure is now more aligned with the expected regional composition.

In the past, Los Queules (LQLES05) displayed a marginally significant difference ($\Delta^+ = 75.5$, $p = 0.077$), suggesting a greater taxonomic breadth than the expected taxonomic structure. However, in the current inventory (LQLES, $\Delta^+ = 62.73$, $p = 0.282$), the observed decrease in taxonomic distinctness was not statistically significant. This reduction in Δ^+ in the current inventories is likely explained by the increased rep-

resentation of *Hymenophyllum* species, as the addition of closely related species within the same genus reduces the average taxonomic distinctness by decreasing the mean distance between species pairs. Other sites did not show significant differences (Tab. 1).

Regarding the variance of taxonomic distinctness (Λ^+), the current inventories ranged from 677.78 at Los Ruiles (LRLES) to 1181.29 at Cerro Ñielol (MNC), the geographically extreme sites of the study area. This pattern suggests a gradual transition from more taxonomically homogeneous to more heterogeneous assemblages, with greater variability in taxonomic distances observed at the northernmost sites (see Tab. S2 and Tab. S4 in Supplementary material).

Despite this apparent gradient, none of the sites exhibited statistically significant differences from the master species list ($\Lambda^+ = 929.52$, $p > 0.05$). However, Cerro Ñielol showed a marginally non-significant difference (MNC, $\Lambda^+ = 1181$, $p = 0.43$), suggesting potential taxonomic enrichment compared to both the master list and the previous inventory (MNC83, $\Lambda^+ = 1024$, $p = 0.087$).

The simultaneous analysis of both indices

(Δ^+ , Λ^+) across five-species intervals identified three statistically distinct zones ($p < 0.05$) in the ellipse plot (Fig. 3a). The central zone represents sites that do not significantly differ from the master species list, based on a 95% confidence threshold.

A clear temporal and spatial pattern emerges, revealing a south-to-north increase in taxonomic complexity that was not evident in previous inventories, indicating a progressive reorganization of site positions. In earlier inventories, LQLESo5 was the most distant from the center, whereas CTM99 was already positioned within the central zone, indicating no differentiation from the master species list. In contrast, the current sampling exhibits a more structured distribution, with CTM, RQE, and MNC now grouped within the central zone, while LRLES is positioned at the extreme.

Overall, this shift indicates a more diverse and structured taxonomic composition in southern sites compared to previous inventories.

Climbers

Taxonomic distinctness in climbers remained stable over time and across sites in both mean (Δ^+) and variance (Λ^+), particularly when compared to epiphytes. The average taxonomic distinctness (Δ^+) for climbers varied slightly, ranging between 70.33 and 72.33, while the variance of taxonomic distinctness (Λ^+) ranged from 117.49 at Los Queules (LQLESo5) to 174.32 at Conculmo (CTM). This suggests a consistent taxonomic structure over both spatial and temporal scales, with no significant differences at any site compared to the master species list ($\Delta^+ = 70.9$, $p > 0.05$).

However, the first inventory at Los Queules (LQLESo5, $\Delta^+ = 72.32$, $p = 0.089$) suggests a minor deviation from the expected taxonomic structure, though this difference was not statistically significant. Compared to the current inventory (LQLES, $\Delta^+ = 72.03$), this indicates that the taxonomic composition of climbers remained relatively unchanged over time at this site.

The simultaneous analysis of both indices (Δ^+ , Λ^+) for the five-species sublists identified five statistically distinct zones ($p < 0.05$) in the ellipse plot (Fig. 3b). Only Conculmo (CTM) was positioned within the central zone, indicating no significant deviation from the master species list at a 95% confidence level.

A clear pattern of increasing taxonomic complexity southwards and over time was observed, alongside a shift in site distribution across the ellipse zones. In the earlier inventories, no sites were positioned within the first or second zone, indicating that none closely resembled the master species list. This suggests that the overall taxonomic structure was historically more simplified. In contrast, the current sampling reveals a general trend of taxonomic enrichment, with some sites shifting towards the central region of the ellipse. For example, LRLESo5 and RQE89, previously

positioned in more peripheral zones, have now moved closer to the center, while no sites remain in the most distant zone.

This shift supports a broader pattern of increasing taxonomic complexity southwards and over time, with sites progressively converging towards the structure represented in the master species list. The presence of five distinct zones in climbing plants confirms that this assemblage encompasses a broader range of genera and exhibits greater phylogenetic dispersion compared to epiphytes, which formed only three zones. This indicates that climbing plant assemblages are taxonomically more heterogeneous, whereas epiphyte communities exhibit greater taxonomic similarity or phylogenetic clustering.

Discussion

Joint use of average taxonomic distinctness and its variance (Δ^+ , Λ^+)

In this study, the average taxonomic distinctness (Δ^+), its variance (Λ^+), and their combined measure (Δ^+ , Λ^+) were analyzed for epiphyte and climbing plant assemblages in five protected wild areas along the native forested coast of central Chile. Although each index individually captures only one dimension of the community's taxonomic structure, the simultaneous use of both indices (represented graphically in an ellipse plot) proved to be more sensitive in detecting significant differences in taxonomic structure than when these indices were assessed separately (Clarke & Warwick 2001). For instance, the combined analysis revealed an overall increase in taxonomic complexity over time for both epiphytes and climbers at most sites, except for Los Ruiles (LRLES), the only site to show a decrease in taxonomic distinctness among epiphytes.

One notable advantage of using both indices concurrently is that Δ^+ offers a consistent and robust measure of taxonomic diversity by quantifying the average variability in taxonomic distances between pairs of species. At the same time, Λ^+ captures the distribution of branches or the shape of the taxonomic tree within the community (Clarke & Warwick 2001). By combining Δ^+ and Λ^+ , researchers can better detect both average changes in taxonomic structure and the variability of these changes. This is particularly valuable for identifying disturbance patterns and differential responses to environmental pressures (Zhou et al. 2010). Consequently, these indices could also be applied to assess potential shifts in taxonomic structure under climate change scenarios.

To date, most studies applying the metrics of taxonomic distinctness have focused on marine and freshwater ecosystems, examining a variety of organisms such as fish, nematodes, benthic macrofauna, and mollusks (Clarke & Warwick 1998, Zhou et al. 2010, Bevilacqua et al. 2011, Jiang et al. 2020). Interest in applying

these metrics to terrestrial ecosystems has grown more recently, with research expanding to environments such as savannas, forest fragments, Mediterranean forests, arid regions, and the effects of silvicultural practices (Silva & Batalha 2006, Selvi et al. 2016, Sferlazza et al. 2023).

The reviewed studies consistently agree that average taxonomic distinctness (Δ^+) and its variance (Λ^+) are valuable tools for assessing taxonomic diversity. Moreover, the simultaneous use of these indices offers several advantages, including greater sensitivity to detecting subtle changes, a multidimensional assessment of taxonomic structure, and enhanced ecological interpretation of community patterns, as highlighted by previous authors (Zhou et al. 2010). However, research within terrestrial ecosystems has yet to fully explore their joint application.

Species richness vs. taxonomic distinctness

Species richness, defined as the total number of species within a community, is a widely used measure of biodiversity, valued for its simplicity and ease of measurement. It facilitates direct comparisons between communities or habitats and helps identify areas of high biodiversity value for conservation (Ellingsen et al. 2005). However, it fails to account for phylogenetic relationships, thereby limiting our understanding of biodiversity at functional and evolutionary scales (Wong et al. 2018). Two communities with the same number of species may differ significantly in their taxonomic composition, leading to variations in ecosystem functionality (Clarke & Warwick 2001).

Taxonomic distinctness metrics, such as Δ^+ and Λ^+ , overcome these limitations by explicitly incorporating taxonomic hierarchy (e.g., genus, family, order) as a proxy for evolutionary relatedness. Although these indices rely on standard taxonomic classifications rather than explicit phylogenetic analyses, they likely capture evolutionary history and functional diversity due to the hierarchical nature of taxonomy. This makes these metrics especially valuable for monitoring ecosystem health and assessing conservation effectiveness (Bevilacqua et al. 2011).

In this study, the taxonomic distinctness is especially evident when comparing epiphytes and climbers. Epiphytes, comprising 20 species, exhibited a broader range of Δ^+ values ($54 < \Delta^+ < 63$), yet the analysis revealed only three distinct zones, indicating that, despite the wider Δ^+ range, their overall taxonomic composition remains relatively cohesive. Climbers, by contrast, have a narrower span of Δ^+ values ($71 < \Delta^+ < 72$) but exhibit higher variability in taxonomic composition, resulting in five distinct zones. Hence, the method demonstrates its sensitivity to differences in community structure, even when the mean Δ^+ varies only slightly, as this sensitivity arises from

the simultaneous consideration of both Δ^+ and its variance Λ^+ , rather than from the average alone.

A key consideration when applying taxonomic distinctness metrics is ensuring that taxonomic classification is well resolved.

While interpreting taxonomic distinctness (Δ^+) and its variance (Λ^+) may be less intuitive than species richness, and comparisons across studies may be hindered by variations in taxonomic resolution or sampling design (Clarke & Warwick 2001), this metric is often more informative, particularly for understanding biodiversity at functional and evolutionary levels (Clarke & Warwick 1998, Jiang et al. 2020, Bevilacqua et al. 2011). Thus, while species richness provides a straightforward measure of biodiversity, it does not necessarily reflect taxonomic structure or phylogenetic relationships. By incorporating taxonomic distinctness metrics, a more accurate and ecologically meaningful picture of biodiversity can be obtained, distinguishing between communities with similar species numbers but different taxonomic compositions.

The challenge of comparing biodiversity over time

Comparing biodiversity over time presents significant methodological and practical challenges that complicate the interpretation of results. A central difficulty is ensuring consistency in sampling design: methodological variations can create a false impression of increased diversity (Lozano et al. 2012) and may partly explain the apparent rise in epiphyte and climber diversity observed in our recent inventories.

Early botanical surveys, though invaluable, were rarely georeferenced or standardized, making strict site-to-site comparisons difficult. Because most historical ecological work lacked the spatial precision and methodological consistency of modern studies (Christie et al. 2019), exact resampling is usually impossible. Even so, these legacy datasets provide indispensable baselines. Comparisons between historical and contemporary inventories are therefore vital for detecting long-term biodiversity trends and disentangling the combined effects of climate forcing and human disturbance (Pereira & Cooper 2006). Indeed, multi-decadal records already document climate-driven declines across a range of animal and plant populations (Morris et al. 2008).

In the absence of continuous monitoring, historical-recent comparisons must be interpreted with caution. Apparent shifts may indeed represent genuine taxonomic turnover, yet the underlying drivers of land-use change, forest dynamics, climate variation, or their interactions often remain unresolved (Plischoff et al. 2012). These uncertainties, together with lingering methodological and taxonomic inconsistencies, can blur the mechanisms behind observed diversity patterns, even when modern surveys follow rigorous, standardized proto-

cols.

An illustration of these challenges arises from our findings. Climbing plants exhibited a marked temporal increase in taxonomic distinctness at all sites except at Cerro Ñielol, where no change was observed. The stability observed at this site may reflect high visitor pressure, estimated to be tens of thousands per year (Subsecretaría de Turismo 2022), though its influence remains unquantified. In contrast, epiphytes showed an overall southward increase in taxonomic distinctness, while Los Ruiles displayed a decline, possibly indicating local homogenization driven by climate-mediated filtering of drought-tolerant lineages. These site-specific patterns underscore how true ecological shifts may be confounded by sampling artifacts and unmeasured pressures, highlighting the importance of rigorously standardized inventories when comparing historical and contemporary datasets.

Taxonomic uncertainty remains a major source of error in temporal biodiversity metrics. Incomplete species-level identifications (Caparrós et al. 2016), recently diverged species complexes (Baumsteiger et al. 2017), cryptic taxa (Kinosian et al. 2020), and erroneous sequences in DNA reference libraries (Sandoval-Sierra et al. 2014) can all mislead analyses. These problems are compounded by the rapid evolution of identification methods. Whereas historical inventories depended on a handful of specialists working with printed floras and herbarium specimens (Bieker & Martin 2018), modern studies draw on millions of observations uploaded to citizen-science platforms such as iNaturalist® (<https://www.inaturalist.org>) and PL@ntNet® (<http://identify.plantnet.org>). This digital revolution has accelerated discovery and broadened coverage, yet large repositories like GBIF still harbor taxonomic inconsistencies, spatial biases, and heterogeneous validation levels that can obscure true biodiversity patterns (Zizka et al. 2019). Such discrepancies must therefore be weighed carefully whenever historical and contemporary datasets are compared.

Well-designed, long-term studies that pair consistent sampling with environmental monitoring remain indispensable for disentangling the interacting drivers of biodiversity change, especially in Latin America and other data-poor regions where standardized time series are rare (Pereira & Cooper 2006, Lindenmayer et al. 2010). In such contexts, legacy inventories provide some of the few baselines available, and taxonomic-distinctness indices offer a practical surrogate for detecting broad-scale shifts in community structure and informing conservation strategies when sustained monitoring is lacking.

Implications for forest conservation

Understanding forest biodiversity demands attention not only to how many species occur, but to how those species

are related. Taxonomic distinctness metrics (Δ^+ and Λ^+) satisfy this requirement by revealing taxonomic loss, homogenization, enrichment, and, ultimately, the resilience of forest communities. Applied to monitoring and restoration, they allow managers to judge whether silvicultural practices preserve an ecologically representative taxonomic structure and, by extension, long-term forest stability.

Epiphytes and climbing plants illustrate the value of this approach. Because epiphytes – especially filmy ferns (*Hymenophyllaceae*) – depend on persistent humidity and shaded micro-habitats, they are highly sensitive to canopy alteration and climatic gradients (Saldaña et al. 2014). Climbers, in contrast, tolerate or even benefit from increased light, thriving in gap environments and spanning a wider range of families (Carrasco-Urra & Gianoli 2009). Monitoring both groups, therefore, yields complementary signals: epiphytes track microclimatic stability and habitat continuity, whereas climbers reflect disturbance regimes, canopy openness, and successional dynamics. Consistent with previous findings (Pincheira-Ulbrich et al. 2018), the present analysis shows that climbers occupy five well-separated zones in the ellipse (Δ^+ , Λ^+), whereas epiphytes cluster in three zones, highlighting their contrasting structural responses.

The greater variability in epiphytic Δ^+ observed suggests heightened sensitivity to fragmentation and forest heterogeneity. Part of this variation may be methodological; minute, filmy ferns are less detectable than conspicuous climbers, and older surveys lacked standard protocols, but it also points to genuine ecological vulnerability. Conversely, the stable taxonomic structure of climbers implies resilience rooted in taxonomic breadth. In our dataset, they span many more families than epiphytes, which concentrate in a few closely related lineages (Silva & Batalha 2006). Such breadth affords functional redundancy that can buffer forests against change.

Climate-driven environmental filtering adds a further layer of complexity. Warming and altered rainfall favor drought-tolerant, phylogenetically clustered taxa (Kutnar et al. 2019), potentially lowering taxonomic distinctness even when species counts remain unchanged. Conversely, when colonization by distantly related species prevails, distinctness may rise (Pincheira-Ulbrich et al. 2018). Either trajectory has functional consequences: greater taxonomic distinctness enhances ecological complementarity, supporting processes such as pollination, seed dispersal, and nutrient cycling. In contrast, phylogenetic homogenization can erode functional redundancy and ecosystem resilience, ultimately compromising those same functions (Elmqvist et al. 2003).

These findings point to clear management priorities. First, conserve humid forest patches that host specialized epiphytic

communities and restore degraded stands in ways that promote the taxonomic variety of climbing plants, thereby strengthening overall forest resilience (Burrascano et al. 2009, Pincheira-Ulbrich et al. 2018). Second, preserve structural heterogeneity: smaller trees provide supports for twiners and tendrils climbers, whereas larger stems are crucial for adventitious-rooted species (Carrasco-Urra & Gianoli 2009). Finally, implement long-term, standardized monitoring, ideally pairing Δ^+ and Λ^+ with environmental variables to track genuine biodiversity trajectories (Silva & Batalha 2006). In this context, citizen-science platforms can help bridge data gaps in regions with limited monitoring capacity (Zizka et al. 2019).

Taken together, these management considerations and monitoring needs underscore the broader significance of the study. In light of these results, although the initial expectation of diverging trends – steady gains in climber diversity and epiphyte decline – were only partially supported, the joint use of Δ^+ and Λ^+ uncovered clear patterns: climbers showed increasing taxonomic distinctness over time and stability along the latitudinal gradient, whereas epiphytes displayed site-specific variability with a southward rise in diversity. These findings confirm that taxonomic-distinctness metrics reveal structural changes that simple species counts may obscure, and reinforce their value for guiding forest-conservation strategies in a changing world.

Conclusions

This study highlights the taxonomic structure of vascular epiphytes and climbing plants in five protected wild areas along the native forested coast of central Chile. Taxonomic distinctness indices (Δ^+ and Λ^+) provided a more nuanced understanding of biodiversity patterns than species richness alone, revealing differences in taxonomic composition and structural complexity.

When applied independently, these indices captured distinct aspects of community structure: average taxonomic distinctness (Δ^+) reflected overall richness across the taxonomic hierarchy, while its variance (Λ^+) highlighted heterogeneity in taxonomic relatedness. Climbing plants exhibited greater taxonomic richness and stability over time and space, with no significant deviations from the expected structure based on the master species list. In contrast, epiphytes, particularly Hymenophyllaceae, showed greater variability, suggesting higher sensitivity to environmental heterogeneity. A trend of increasing epiphyte taxonomic complexity was observed towards the south, whereas Los Ruiles exhibited signs of taxonomic simplification, potentially indicating biodiversity loss or climate-induced changes.

The simultaneous use of Δ^+ and Λ^+ improved the detection of taxonomic shifts, showing that most sites became more structured over time. However, differences

in sampling methodologies across historical and contemporary inventories may have influenced some patterns, requiring cautious interpretation of temporal comparisons.

These findings underscore the importance of maintaining structural forest heterogeneity to support taxonomically diverse assemblages. Epiphytes serve as indicators of forest continuity and microclimatic stability, while climbing plants reflect disturbance regimes and successional dynamics.

Future research should standardize sampling methods and integrate taxonomic distinctness metrics with functional and environmental data to enhance forest biodiversity assessments and conservation planning.

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Supplementary Material

Tab. S1 - Epiphyte presence/absence matrix across five protected areas in central Chile.

Tab. S2 - Taxonomic classification of epiphyte species recorded across five protected areas in central Chile.

Tab. S3 - Climbing plant presence/absence matrix across five protected areas in central Chile.

Tab. S4 - Taxonomic classification of climbing plant species recorded across five protected areas in central Chile.

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