

Integrating forest structure and livestock use to assess regeneration and understory responses in *Austrocedrus chilensis* forests

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Abstract

Austrocedrus chilensis forests in Argentine Patagonia support overlapping uses of timber production and livestock grazing, generating a wide range of structural conditions associated with contrasting land-use histories. We used a physiognomic framework based on eight forest physiognomies to evaluate how forest structural context and a dung-based livestock use index (LUI) were associated with tree regeneration and understory plant communities across 95 sampled stands. All structural variables differed significantly among physiognomies. LUI has been positively associated with the probability of browsing damage and negatively associated with sapling slenderness, consistent with morphological effects of browsing. Regeneration density declined significantly with increasing LUI in the open physiognomies (physiognomy $\times$ LUI interaction), indicating that the association between livestock use and regeneration density was physiognomy-dependent. Native understory richness, diversity, and evenness declined significantly with increasing LUI ($p < 0.05$), while exotic species diversity was more strongly associated with forest physiognomy, particularly with more open physiognomies, than with LUI. Physiognomies with intermediate structural complexity showed comparatively high native diversity. These findings indicate that livestock use was associated with *A. chilensis* regeneration and understory composition both independently of forest structural context and, for regeneration density, in a manner that depends on it. The physiognomic framework provides an operational basis for integrating forest structure into adaptive management of *A. chilensis* forests and may be applicable to other temperate forest systems subject to interacting land uses.

1 Introduction

Forest stand dynamics and structural heterogeneity arise from interactions among natural disturbances and land-use history (Mitchell et al. 2023; Jiang 2026). Forest harvesting, in particular, can alter the trajectory of ecosystem dynamics, by simplifying or diversifying forest structure, depending on management objectives and ecological characteristics of each stand (Kuuluvainen 2002; Kimmins 2003; Wang et al. 2025). In ecosystems under multiple land uses, the overlap of productive activities can simplify forest structure, especially when uses occur simultaneously without integrated planning (Hobbs and Huenneke 1992; Massó Estaje et al. 2026; Simensen 2026). More recently, this perspective has converged with approaches emphasizing resilience and the conservation of natural structural variability (Kuuluvainen 2002; McElhinny et al. 2005; Pickering et al. 2025). Structural heterogeneity across spatial scales is increasingly recognized as an important driver of forest ecosystem functioning and provision of ecosystem services (Sun et al 2025; Hernández-Moreno et al 2026).

In *Austrocedrus chilensis* (D. Don) Pic. Serm & Bizzarri forests of northern Patagonia (Argentina), the long history of timber harvesting and livestock grazing has been associated with high structural heterogeneity at both stand and landscape scales, ranging from dense closed-canopy forests to open woodlands with only a few remnant trees (Dezzotti and Sancholuz 1991; Carabelli 2006). Timber harvesting has promoted the spatiotemporal overlap of natural disturbances and other land uses, particularly livestock grazing. Combined with weak institutional governance and fragmented land-use planning, these interactions have contributed to a mosaic of contemporary forest structural conditions (Veblen et al 1992; Garcia and Burns 2022; Hernández-Moreno et al. 2023; Bava and Caselli 2025). In this context, forest physiognomies provide an operational framework for integrating forest structure, regeneration dynamics, understory composition, and grazing intensity within a common ecological context. Classifying stands into forest physiognomies facilitates the analysis and interpretation of ecological responses and supports management across heterogeneous forest conditions (McElhinny et al 2005; Caviedes and Ibarra 2017; Sun et al 2025).

Despite the availability of silvopastoral management guidelines for northern Patagonian forests and silvicultural proposals focused on regeneration dynamics (Gobbi 2007; Loguercio et al. 2024), questions remain about how forest structure, regeneration, and understory diversity interact under different grazing intensities in *A. chilensis* forests. Previous studies have documented the effects of livestock grazing on individual ecosystem components, such as tree regeneration and understory floristic composition (Relva and Veblen 1998; Arpigliani et al. 2024, 2025), but approaches that explicitly integrate forest structure with contemporary grazing remain scarce, despite these processes operating simultaneously within the same stands. However, management decisions are ultimately made at the stand scale, where forest structure provides the ecological context in which regeneration dynamics and understory responses are interpreted in relation to grazing. This highlights the need for an integrative framework that uses quantitative forest structure as the ecological basis for analysing the relationships among regeneration, understory vegetation and grazing, while supporting management decisions across contrasting stand conditions. Moreover, livestock grazing is spatially heterogeneous across these forest landscapes due to limited ranch infrastructure, steep slopes, rough terrain, and distance to water sources (Quinteros 2018; Trinco et al. 2025).

To address this gap, we adopted a physiognomic framework in which quantitative forest structure provides the ecological context for interpreting regeneration responses and understory vegetation under heterogeneous grazing conditions. We hypothesized that forest physiognomy and livestock use are jointly associated with tree regeneration and understory plant communities, but through different ecological mechanisms. Specifically, we expect that: (i) increasing livestock use would be associated with increased browsing damage on *A. chilensis* regeneration and with morphological changes in saplings, whereas regeneration density would be primarily associated with forest

physiognomy; (ii) native understory richness, diversity, and evenness would decline with increasing livestock use, whereas exotic species would become more frequent under structurally open physiognomies; and (iii) forest physiognomy would provide the structural context for interpreting these responses by representing differences in canopy cover, stand occupancy, and developmental stage across the landscape. Accordingly, the objective of this study was to evaluate how livestock use is associated with forest regeneration and understory plant communities across contrasting forest physiognomies. Specifically, we aimed to: (i) evaluate associations of forest physiognomy and livestock use with tree regeneration using indicators of establishment (density), immediate impact (damage index), and cumulative morphological response (slenderness index); and (ii) assess how forest physiognomy and livestock use influence understory plant species richness, diversity, and evenness, with separate analyses for native and exotic species.

2 Materials and methods

2.1 Study area

The study was conducted in *A. chilensis* dominated forests located between the Río Manso valley (41° SL) and 42° SL in Río Negro province, Argentina (Fig. 1). These forests develop along a pronounced west-to-east climatic gradient characterized by decreasing annual precipitation and increasing mean temperature (Dezzotti and Sancholuz 1991; Pastorino et al. 2006). A total of 95 sampling locations were selected across the study area to encompass the range of forest structural conditions. To minimize environmental variation among sampled stands, we restricted the study to areas between 900 and 1500 mm yr⁻¹ isohyets (Bianchi et al. 2016) and excluded south-facing slopes because of their cooler, lower-radiation microclimate conditions.

Sampling locations were selected to represent contrasting forest structural conditions and avoiding stand edges, roads, streams, and other disruptive landscape features. Field surveys were combined with visual interpretation of high-resolution remote sensing imagery to confirm that selected stands were embedded within an *A. chilensis* forest matrix, explicitly excluding naturally open forests associated with edaphic or geomorphological conditions. Also, we delineated stand boundaries based on changes in canopy texture, encompassing at least 1 hectare of relatively homogeneous forest structure in each case. Sampling was conducted during the austral summer, between December and February of 2023–2024, and forest vegetation, understory vegetation, tree regeneration, and dung counts were recorded during the same field visit.

2.2 Forest physiognomic framework and sampling methods

Based on quantitative structural attributes and previous descriptions of stand structure, disturbance history, and forest developmental conditions reported for *A. chilensis* forests (Dezzotti and Sancholuz 1991; Veblen et al. 1992; Carabelli et al. 2006; Gobbi 2007; Burns et al. 2013; Trinco et al. 2021; Arpigliani et al. 2025), we defined eight forest physiognomies representing discrete structural conditions along a gradient from dense closed-canopy forests to highly simplified parkland environments (Fig. 2). These physiognomies were established as the structural framework for the study as follows.

Closed forests, characterized by continuous canopy cover and small or absent gaps, include four physiognomies: Maximum stand occupancy (MS) (n = 6), stands where site resources are fully occupied by trees of either very high density or large size, resulting in the highest basal area of the gradient; Active stem exclusion (AE) (n = 8), even-aged stands of uniform small-diameter trees in full competitive exclusion, with a very closed canopy and no gap dynamics; Late stem exclusion (LE) (n = 14), stands where density-dependent mortality is at its highest, showing incipient canopy openings; and Understory reinitiation (UR) (n = 11), mature stands where surviving dominant trees sustain high basal area at lower densities, and small recurring gaps allow a diverse regeneration layer to develop. Open forests, characterized by a partially open canopy with large gaps, include two physiognomies: Cohort mixing (CM) (n = 17), structurally complex stands where trees of different sizes and ages coexist as a result of recurrent natural disturbances or moderate selective harvesting, generating a heterogeneous light environment that supports regeneration at multiple stages; and Open woodland (OW) (n = 22), stands where a significant reduction in tree density from harvesting has left scattered large-diameter remnant trees, producing extensive canopy openings. Parkland environments, characterized by a predominantly herbaceous matrix with isolated or grouped trees, include two physiognomies: Parkland remnant (PR) (n = 8), open stands where the tree component is sparse and spatially aggregated, and regeneration is restricted to microsites protected from herbaceous competition; and Pastoral clearing (PC) (n = 9), the most structurally simplified physiognomy, where tree cover is virtually absent and the regeneration cycle is completely disrupted.

These physiognomies encompass a broad spectrum of land-use histories, ranging from unmanaged closed-canopy stands to structurally simplified stands resulting from past thinning operations and intensive harvesting (Fig. 3), all embedded within a livestock production context.

The stand was considered the primary sampling unit because the study focused on stand-level associations among forest physiognomy, livestock use, regeneration, and understory vegetation. Although multiple stands could occur within the same broader property or landscape sector, the minimum separation distance of 200 m between sampled stands was maintained to reduce local spatial dependence.

2.3 Field sampling

At each stand we established a 50-m transect following the dominant slope. Hemispherical photographs were taken at both ends of each transect at a height of 1.5 m using a fisheye lens and Gap Light Analyzer software (Frazer et al. 1999) to estimate canopy openness (CO, %). Forest structure was assessed using the Bitterlich angle-count method, recording diameter at breast height (DBH, cm), tree species, and tree status (live or dead) for trees with DBH > 10 cm. Natural tree regeneration was assessed in two strata: (i) initial regeneration (< 1.6 m height) using rectangular variable-area plots (2.5–20.0 m²) established at each end of the 50-m transect. Plot size was selected based on a rapid visual assessment of expected local abundance, when fewer than three individuals were present in the maximum 20 m² plot, all individuals recorded were retained; and (ii) advanced regeneration (≥ 1.6 m height and DBH < 10 cm) using fixed-area plots of 20 m². For initial regeneration, we recorded density (RD, plants ha⁻¹), height (H, cm) and basal diameter (BD, cm), browsing damage by counting damaged branches and apical status (browsed or unbrowsed). Based on these measurements, following Arpigiani et al. (2022), we calculated a browsing damage index (BDI) for each stand as

$$BDI = \left(\frac{n^{\circ} \text{ of damaged individuals}}{\text{total } n^{\circ} \text{ of individuals}} \right) + \left(\left(\frac{n^{\circ} \text{ of damaged branches}}{\text{total } n^{\circ} \text{ of branches}} \times 0.4 \right) + \left(\frac{n^{\circ} \text{ of damaged apical bud}}{\text{total } n^{\circ} \text{ of individuals}} \times 0.6 \right) \right)$$

On the other hand, the slenderness index (SI) was used as a morphological trait describing the relative relationship between sapling height and basal stem diameter, and was calculated as

$$SI = \left(\frac{H}{BD} \right)$$

To characterize the understory layer, we conducted a point-intercept sampling along each transect. Plants < 2 m in height were recorded at 1 m intervals, documenting species identity and origin (native or exotic). Each contact point was considered a species occurrence. Species richness (S) was calculated as the total number of species recorded per stand, both for the entire plant community and separately for native and exotic species. These data were used to estimate: (i) the Shannon-Wiener diversity index (H') which integrates species richness and relative abundance, reflecting both species number and dominance patterns (Shannon 1948); and (ii) Pielou's evenness index (J') which standardizes H' by species richness. Both indices were calculated for the complete community and separately for native or exotic subsets.

Livestock use intensity was estimated using a livestock use index (LUI, cattle equivalents·ha⁻¹) based on dung counts following the methodology proposed by Martínez Pastur et al. (2022). The index assumes that defecation rates are relatively constant within each stand and throughout the year — cattle producing 14 faeces·day⁻¹ (Aland et al. 2002; Phillips 2002; Hirata et al. 2011), sheep 13 faeces·day⁻¹ (Haynes and Williams 1993), and horses 8.5 faeces·day⁻¹ (Westendorf and Krogmann 2013; Westendorf 2020) — and that dung remains identifiable in the field for approximately one year under local climatic conditions, allowing dung density to be converted into a stand-level estimate of recent livestock use intensity. To allow comparisons among species, counts were standardized as cattle equivalents (CE) using the following conversion factors: 1 CE = 6.25 sheep = 0.625 horses (Haynes and Williams 1993; Westendorf 2020). We acknowledge that this method captures livestock use over approximately one year prior to sampling and may be subject to spatial aggregation of dung near trails or water sources; it should therefore be interpreted as a proxy for recent rather than long-term grazing history.

2.4 Statistical analyses

Differences among physiognomies in structural attributes and regeneration variables were evaluated using one-way ANOVA followed by Tukey's HSD tests or Kruskal–Wallis tests followed by Dunn's post hoc comparisons with Bonferroni correction, depending on data distribution (Table 1). The physiognomic framework was subsequently used as the structural context for evaluating patterns of tree regeneration and understory plant communities across the livestock use gradient.

To account for potential spatial dependence among sampled stands within the same landscape sector, sampled stands were grouped into seven landscape sectors defined a priori according to watershed boundaries and land-use history, independently of forest structural condition. A sector was therefore included as a random intercept in all stand- and sapling-level generalized linear mixed models (GLMMs). The association between LUI and browsing damage was evaluated using BDI. Because BDI contained a large number of zeros, browsing responses were analysed using a two-stage hurdle approach. First, browsing occurrence (damaged vs. undamaged saplings) was analysed using a binomial GLMM (Model 1). Second, browsing severity was analysed using a Gamma GLMM, fitted only to damaged individuals (Model 2). We also evaluated the association between BDI and SI. Since SI was continuous and right-skewed, a Gamma GLMM was fitted,

including sector and stand nested within sector as random intercepts (Model 3). A second-order polynomial term for BDI was included to account for potential non-linear associations between browsing intensity and SI, given that BDI was calculated at the stand level and assigned to all saplings within each stand.

The combined association of forest physiognomy (P) and LUI with SI was evaluated using a Gamma GLMM with the same nested random-effect structure (Model 4). Finally, initial *A. chilensis* regeneration was analysed using a two-stage modelling approach. Regeneration occurrence was evaluated using a binomial GLMM (Model 5a), excluding physiognomies in which regeneration was completely absent. Regeneration density was analysed only for stands where regeneration was present using a Gamma GLMM (Model 5b). For all models including both forest P and LUI (Models 4, 5a, and 5b), an initial model containing the $P \times LUI$ interaction was initially fitted. When the interaction was not statistically supported ($p > 0.05$), it was removed and the final model was refitted using only additive effects, providing a more parsimonious description of the observed associations (Table 2).

The association of P and LUI with understory plant diversity was evaluated using species richness (S), the Shannon diversity index (H'), and Pielou's evenness index (J'), each calculated separately for the total, native, and exotic components of the understory flora, resulting in nine response variables (Models 6–14). Because sample size varied among these subsets, full richness and H' models were fitted using all sampled stands ($n = 95$), whereas J' and exotic-flora models were restricted to stands where the corresponding taxa were present. Model distributions were selected according to the scale and distributional properties of each response variable, as assessed through exploratory analyses and residual diagnostics. S was analysed using negative binomial GLMMs; H' was analysed using Gamma GLMMs for the total community and Gaussian GLMMs for the native and exotic components, the latter fitted on log-transformed values where residual diagnostics indicated a better fit. J' was analysed using Beta GLMMs because the index is bounded between 0 and 1. All models included sector as a random intercept, following the same rationale adopted for the regeneration analyses. An initial model containing the $P \times LUI$ interaction was first fitted, interaction terms were retained only when statistically supported ($p \leq 0.05$), otherwise the additive model was reported as final. For two exotic-flora models (H' and J'), one or more physiognomy $\times$ LUI interaction terms were dropped due to rank deficiency, reducing the associated degrees of freedom (Supplementary Material Table S1).

Model fit was assessed using DHARMA simulated residuals for all models. Effect sizes were estimated using marginal pseudo- R^2 following Nakagawa and Schielzeth for models 2, 3, 4, 5b, and 6–14; Tjur's R^2 and classification accuracy for the binomial occurrence for models 1 and 5a. Post-hoc comparisons among physiognomies were conducted using estimated marginal means with Tukey adjustment. All analyses were conducted in R software (R Core Team 2024).

3 Results

All structural variables differed significantly among the eight physiognomies (Table 1). Live basal area (BA) showed the strongest differentiation ($p < 0.001$), spanning the full gradient from PC, where BA was virtually absent ($3.7 \pm 3.0 \text{ m}^2\cdot\text{ha}^{-1}$) through PR ($16.3 \pm 3.5 \text{ m}^2\cdot\text{ha}^{-1}$) and the open forest physiognomies (OW and CM; 35.5 ± 6.3 and $32.5 \pm 5.1 \text{ m}^2\cdot\text{ha}^{-1}$, respectively), to the closed forest physiognomies where BA increased progressively and reached its maximum in MS ($73.5 \pm 6.7 \text{ m}^2\cdot\text{ha}^{-1}$). Tree density (TD) also differed markedly among physiognomies ($p < 0.001$), with the highest values in MS ($1863 \pm 856 \text{ trees}\cdot\text{ha}^{-1}$) and AE ($1486 \pm 149 \text{ trees}\cdot\text{ha}^{-1}$), representing the densest stand conditions along structural gradient, intermediate in LE ($921 \pm 225 \text{ trees}\cdot\text{ha}^{-1}$), UR ($923 \pm 214 \text{ trees}\cdot\text{ha}^{-1}$) and CM ($718 \pm 148 \text{ trees}\cdot\text{ha}^{-1}$), and lowest in OW ($380 \pm 110 \text{ trees}\cdot\text{ha}^{-1}$), PR ($422 \pm 244 \text{ trees}\cdot\text{ha}^{-1}$) and PC ($47 \pm 34 \text{ trees}\cdot\text{ha}^{-1}$), where isolated or scattered remnant trees constitute the only tree structural component. Canopy openness (CO) followed the opposite pattern with respect to BA and TD ($p < 0.001$), with PC presenting the highest values ($64.3 \pm 9.2\%$) and AE the lowest ($7.1 \pm 2.3\%$), PR occupied an intermediate position ($26.3 \pm 5.2\%$), while CM ($17.0 \pm 5.5\%$) and OW ($14.7 \pm 4.2\%$) showed greater within-group variability than the remaining physiognomies, consistent with more heterogeneous canopy structures and large canopy gaps. Quadratic mean diameter (QMD) also differed among physiognomies ($p < 0.001$), although without a consistent gradient. The highest values occurred in OW ($34.6 \pm 4.5 \text{ cm}$), consistent with stands dominated by fewer, larger trees, whereas AE showed the lowest QMD ($21.3 \pm 2.0 \text{ cm}$), which, together with its high BA and TD, is consistent with dense, relatively even-aged stands in the active stem exclusion stage. The remaining physiognomies displayed intermediate QMD values.

Regeneration variables differed significantly among physiognomies, though with greater within-group variability than structural variables. Initial regeneration density (IR) differed among physiognomies ($p < 0.001$), being highest in UR and LE (7205 ± 15766 and $6750 \pm 8759 \text{ trees}\cdot\text{ha}^{-1}$, respectively), consistent with episodic recruitment patterns expected under gap dynamics and mortality-created microsites, and absent in PC ($0 \text{ trees}\cdot\text{ha}^{-1}$), consistent with the absence of an active regeneration cycle. Advanced regeneration (AR) also differed significantly among physiognomies ($p < 0.001$), with LE showing the highest values ($3464 \pm 4749 \text{ trees}\cdot\text{ha}^{-1}$) and OW and PC the lowest (625 ± 654 and $56 \pm 107 \text{ trees}\cdot\text{ha}^{-1}$, respectively), suggesting limited progression toward more densely forested conditions in the most open physiognomies.

Table 1

Structural characterization of the eight *Austrocedrus chilensis* forest physiognomies (n = 95 stands). MS = maximum stand occupancy, AE = active stem exclusion, LE = late stem exclusion, UR = understory reinitiation, OW = open woodland, CM = cohort mixing, PR = parkland remnant, PC = pastoral clearing. Different lowercase letters within each column indicate significant differences among physiognomies (post-hoc tests following Kruskal-Wallis or one-way ANOVA; $p < 0.05$). CO = canopy openness, BA = live basal area, TD = tree density, QMD = quadratic mean diameter, IR = initial regeneration density, AR = advanced regeneration density. Asterisks indicate the test used: = *Kruskal-Wallis, **ANOVA.

Physiognomy	CO (%)**	BA (m ² .ha ⁻¹)**	TD (trees.ha ⁻¹)**	QMD (cm)**	RI (trees.ha ⁻¹)*	RA (trees.ha ⁻¹)*
MS	9.15ab	73.5f	1863.2e	23.4ab	2291.6ab	2208.3ac
AE	7.10a	56.3e	1486.5e	21.3a	3531.2a	1843.7ac
LE	9.30a	40.8d	921.7d	23.2a	6750a	3464.3c
UR	10.4ab	52.0e	923.5d	26.8ab	7204.5a	931.81abc
CM	17.0c	32.5c	718.1cd	23.4a	4573.5a	1411.7ac
OW	14.7bc	35.5c	380.9b	34.6c	3297.7a	625.0ab
PR	26.3d	16.3b	422.9abc	23.6a	1781.2ab	1500.0abc
PC	64.3e	3.7a	47.2a	30.9bc	0.0b	55.5b
Statistic (p)	152.9 (< 0.001)	191.8 (< 0.001)	43.33 (< 0.001)	13.0 (< 0.001)	26.09 (< 0.001)	35.54 (< 0.001)

Estimated LUI values across sampled stands ranged from 0 to 2.95 cattle-equivalents·ha⁻¹, although high stocking rates were recorded in relatively few stands. The occurrence and severity of browsing damage on initial regeneration varied markedly among stands. Hurdle models indicated that LUI was significantly associated with the probability of browsing damage occurrence (Model 1: $\chi^2=4.69$, $p = 0.030$), with higher livestock use increasing the likelihood of browsing, but was not significantly associated with damage severity once browsing had occurred (Model 2: $\chi^2=2.95$, $p = 0.086$) (Table 2). SI was significantly related to BDI (Model 3) (Table 2), exhibiting a quadratic response in which the highest slenderness values were observed in undamaged individuals; this quadratic relationship between BDI and SI is consistent with morphological changes associated with repeated browsing.

When SI was analyzed as a function of forest P and LUI (Model 4), both terms were significantly associated with SI (physiognomy: $\chi^2=14.96$, $p = 0.037$; LUI: $\chi^2=41.01$, $p < 0.001$), with no significant P×LUI interaction ($\chi^2=8.46$, $p = 0.294$), indicating that the association between LUI and SI was consistent across physiognomies. Tukey-adjusted post-hoc comparisons across all physiognomy pairs detected only a significant difference between CM and PC (mean 61.7 ± 3.46 cm and 95.1 ± 12.46 cm, respectively), indicating that the physiognomy effect was driven mainly by this contrast rather than by broad differentiation across the full structural gradient. LUI was negatively associated with SI ($\beta=-0.530 \pm 0.083$), indicating that regeneration became progressively less slender with increasing LUI, irrespective of physiognomy.

Finally, initial *A. chilensis* regeneration was evaluated using a two-stage approach. LUI was not significantly associated with the probability of regeneration occurrence (Model 5a: $\chi^2=2.01$, $p = 0.157$), but was significantly and negatively associated with regeneration density in stands where regeneration was present (Model 5b: $\chi^2=13.04$, $p < 0.001$), and this association differed among physiognomies (P×LUI interaction: $\chi^2=13.75$, $p = 0.033$). Physiognomy-specific slopes indicated that the negative association between LUI and regeneration density was strongest in the PR ($\beta=-2.86 \pm 0.79$, $p < 0.001$) and UR ($\beta=-6.12 \pm 2.45$, $p = 0.012$) physiognomies, while slopes did not differ significantly from zero in the remaining physiognomies.

Together, these results indicate that LUI was associated with an increased probability of browsing damage and reduced sapling slenderness, and was negatively associated with regeneration density in a physiognomy-dependent manner, while showing no significant association with regeneration occurrence or browsing damage severity.

Table 2

Models used to evaluate the associations of livestock use index (LUI) and forest physiognomy (P) with *Austrocedrus chilensis* regeneration. For each model, the response variable, predictor, sample size (n), model type, distribution and link function, test statistic, p-value, effect size, and estimator ($\pm$ SE) are presented. Hurdle models (1–2, 5a–5b) show two components: probability of occurrence (binomial, logit) and magnitude of response (Gamma, log). Models 4, 5a, and 5b tested a $P \times$ LUI interaction, retained only when significant ($p \leq 0.05$). All models included sector as a random intercept and were validated with DHARMA simulated residuals. BDI = browsing damage index, DO = damage occurrence, RD = regeneration density, RO = regeneration occurrence, SI = slenderness index, R^2_m = marginal R^2 , A = classification accuracy, $R^2_T = R^2_{Tjur}$.

Model	Response	Predictor	n	Distribution and link function	χ^2	df	p-value	Effect size	Random effects (ICC)	Estimator $\pm$ SE
(1) GLMM	DO	LUI	87	Binomial (logit)	4.69	1	0.030	$R^2_T = 0.19$ (A = 0.747)	Sector = 0.19	$\beta = 1.548 \pm 0.715$
(2) GLMM	BDI	LUI	44	Gamma (log)	2.95	1	0.086	$R^2_m = 0.08$	Sector = 0.00	$\beta = 0.455 \pm 0.265$
(3) GLMM	SI	BDI	695	Gamma (log)	26.01	1	< 0.001 (*)	$R^2_m = 0.07$	Sector = 0.002	$\text{poly}_1 = -2.271 \pm 0.445$
					9.92	1	0.002 (*)		Stand = 0.37	$\text{poly}_2 = -1.053 \pm 0.334$
(4) GLMM Additive	SI	P	695	Gamma (log)	14.96	7	0.037 (*)	$R^2_m = 0.23$	Sector = 0.01	Post-hoc (physiognomy)
		LUI			41.01	1	< 0.001 (*)		Stand = 0.29	$\beta = -0.530 \pm 0.083$
		P : LUI			8.46	7	0.294		–	–
(5a) GLMM Additive	RO	P	86	Binomial (logit)	5.40	7	0.494	$R^2_T = 0.19$ (A = 0.802)	Sector = 0.09	–
		LUI			2.01	1	0.157			$\beta = -1.620 \pm 1.143$
		P : LUI			5.63	7	0.466		–	–
(5b) GLMM With interaction	RD	P	68	Gamma (log)	9.20	6	0.163	$R^2_m = 0.37$	Sector = 0.17	–
		LUI			13.04	1	< 0.001 (*)			$\beta = -7.612 \pm 4.081$
		P : LUI			13.75	6	0.033 (*)			–

Understory plant diversity was associated with both P and LUI, although the strength and direction of these associations differed for native and exotic species (Supplementary Material Table S1). No significant $P \times$ LUI interaction was detected for any of the nine understory response variables (all $p > 0.10$), indicating that the association between LUI and understory diversity was broadly consistent across physiognomies. S for all species differed significantly among physiognomies ($\chi^2=15.42$, $p = 0.031$) (Fig. 4.A) but was not significantly associated with LUI ($\chi^2=1.41$, $p = 0.236$). When considering native and exotic species separately, native S differed significantly among P ($\chi^2=20.58$, $p = 0.004$) (Fig. 4.A) and declined with increasing LUI ($\beta=-0.275 \pm 0.129$, $\chi^2=4.59$, $p = 0.032$) (Fig. 4.B), while exotic S differed among P ($\chi^2=25.61$, $p < 0.001$) but showed no significant relationship with LUI ($\chi^2=0.38$, $p = 0.538$).

H' for the total community differed significantly among P ($\chi^2=14.80$, $p = 0.039$) (Fig. 4.C) and was negatively associated with increasing LUI ($\beta=-0.158 \pm 0.060$, $\chi^2=7.00$, $p = 0.008$) (Fig. 4.D). This pattern was more pronounced for native species, whose H' also differed significantly among P ($\chi^2=14.50$, $p = 0.043$) (Fig. 4.C) and showed a stronger negative association with LUI ($\beta=-0.415 \pm 0.120$, $\chi^2=11.92$, $p < 0.001$) (Fig. 4.C). In contrast, exotic species H' differed significantly among P ($\chi^2=28.31$, $p < 0.001$) (Fig. 4.C), with higher values in open physiognomies, but showed no significant association with LUI among stands where exotic species were present ($\chi^2=0.05$, $p = 0.817$).

J' for the total community and for native species did not differ significantly among P ($\chi^2=4.15$, $p = 0.762$ and $\chi^2=3.14$, $p = 0.872$, respectively), but was negatively associated with increasing LUI ($\beta=-0.442 \pm 0.124$, $p < 0.001$ and $\beta=-0.589 \pm 0.180$, $p = 0.001$, respectively) (Fig. 4.F),

indicating a progressive dominance of a smaller subset of species at higher levels of livestock use. In contrast, exotic species evenness differed significantly among physiognomies ($\chi^2=23.69$, $p = 0.001$) (Fig. 4.E), with lower values in the closed-canopy physiognomies (LE, AE, MS), but showed no significant association with LUI ($\chi^2=1.71$, $p = 0.191$). Overall, native understory diversity and evenness were negatively associated with LUI, whereas patterns of exotic species diversity and evenness were more strongly associated with forest physiognomy than with LUI, and none of these associations depended on physiognomic context.

4 Discussion

4.1 Associations of livestock use and forest structure on regeneration and understory communities

The observed heterogeneity in LUI reflects differences in grazing intensity associated with topography, accessibility, land-use history, and traditional livestock management, consistent with previous studies from northern Patagonia (Arias Sepúlveda and Chillo 2017; Joelson et al. 2025). In our study, LUI was associated with *A. chilensis* regeneration through cumulative morphological changes in saplings, and, in a physiognomy-dependent manner, reduced regeneration density. The negative relationship between LUI and SI, together with the association between SI and BDI, is consistent with repeated herbivory being associated with reduced vertical growth and modified sapling architecture, potentially decreasing the ability of individuals to compete for light during later developmental stages. This morphological response is consistent with that reported by Arpigliani et al. (2022) for mixed *A. chilensis*-*N. dombeyi* forests under livestock use within the study region. Likewise, global meta-analyses have reported generally negative associations between livestock grazing and tree regeneration, although with considerable variability depending on livestock type, grazing intensity, and environmental context (Wadud et al. 2024). On the other hand, the positive association we detected between LUI and the probability of browsing damage occurrence was consistent with the relationship reported by Relva and Veblen (1998) for *A. chilensis* regeneration. Regeneration density, in turn, was not associated with LUI as a main effect, but declined significantly with increasing LUI specifically in PR and UR physiognomies. This pattern departs from our initial expectation that regeneration density would be primarily structured by forest physiognomy independently of livestock use; instead, physiognomy appears to condition where LUI has a detectable association with regeneration density, rather than substituting for it. This does not necessarily imply that recruitment is unrelated to livestock grazing in closed physiognomies, but rather that any association there may be weaker, more variable, or dependent on additional environmental factors not captured at the spatial and temporal scale evaluated here. Previous studies indicate that livestock exclusion alone does not guarantee successful tree regeneration (Arpigliani et al. 2024; Sánchez-Jardón et al. 2026), suggesting that soil conditions, light availability, and vegetation competition may become limiting once browsing pressure is reduced. Similarly, Trinco et al. (2024) reported that continuous herbaceous cover restricts *A. chilensis* establishment, a mechanism that may contribute to the scarce regeneration observed in parkland environments (PR and PC), and that may also help explain why the association between LUI and regeneration density was detectable precisely in these more open, herbaceous-dominated conditions.

Taken together, our results indicate that LUI was associated with *A. chilensis* regeneration both through browsing-related morphological responses that were broadly consistent across physiognomies, and through reductions in regeneration density that were concentrated in structurally open physiognomies. The observed variation in sapling architecture, together with environmental constraints reported by previous studies (Carabelli et al. 2006; Gobbi 2007; Trinco et al. 2024; Joelson et al. 2025), may compromise sapling survival and long-term development. This interpretation is consistent with the population dynamics models of Arpigliani et al. (2025), who predicted gradual declines in sapling abundance in mixed *A. chilensis*-*N. dombeyi* forests under higher silvopastoral use. The context-dependent nature of grazing impacts highlighted by global syntheses (Öllerer et al. 2019), and illustrated here by the physiognomy-dependent association between LUI and regeneration density, reinforces the importance of evaluating regeneration responses together with forest structure and local environmental conditions. Within this context, the physiognomic framework adopted in this study provides a useful basis for interpreting how variation in land-use history, canopy structure, light availability, and vegetation competition is associated with regeneration patterns across heterogeneous forest stands.

The understory community exhibited contrasting associations of native and exotic species with LUI and forest physiognomy. Native species richness and Shannon diversity declined significantly with increasing LUI, and evenness followed the same pattern, indicating that higher livestock use was associated with progressive dominance by a subset of tolerant species rather than a uniform reduction across the flora. This pattern is consistent with studies from temperate forest grazing systems reporting lower native plant diversity under higher grazing pressure and a greater prevalence of grazing-tolerant and disturbance-adapted species (Vázquez 2002; Piazza et al. 2016; Joelson et al. 2025; Rodríguez et al. 2026). In contrast, Arpigliani et al. (2024) found no significant differences in richness or diversity between grazed and ungrazed mixed *A. chilensis*-*N. dombeyi* forests. This discrepancy may reflect the broader livestock use gradient represented in our study, which may capture patterns that are less evident across the narrower grazing conditions evaluated in that study.

Unlike native species, exotic S and H' were not significantly associated with LUI but differed consistently among forest physiognomies, with higher values in open physiognomies and lower or absent in closed forests (Fig. 4A and 4C). This pattern suggests that exotic species were more frequently associated with structural open forests conditions than with the grazing intensity, consistent with the idea that greater light availability, reduced canopy cover, and reduced competition from native species in these physiognomies determine whether exotic propagules can successfully establish (Carabelli et al. 2006; Sánchez-Jardón et al. 2010; Martínez Pastur et al. 2022). The absence of a significant relationship with LUI, even among sites where exotics species were present, suggests that the range of livestock use documented in this study was not associated with detectable differences in exotic diversity. Alternatively, any association between LUI and exotic establishment may operate over longer temporal scales than captured by this cross-sectional study. Although livestock grazing has often been linked to exotic plant invasion in grazed forest ecosystems (Vázquez 2002; Piazza et al. 2016), our results indicate that, within *A. chilensis* forests, exotic species distribution was more closely associated with forest physiognomy than with contemporary LUI.

Native S and H' remained relatively high across most forest physiognomies, including both closed and open forests, but declined markedly in the most structurally simplified condition (PC) (Fig. 4A and 4C). This pattern is consistent with previous observations in *A. chilensis* forests (Carabelli et al. 2006), as well as with broader studies from temperate forests reporting high understory diversity under intermediate levels of structural complexity and canopy cover (Sánchez-Jardón et al. 2010; Martínez Pastur et al. 2022). The lower native diversity observed in PC suggests that beyond a certain level of structural simplification, reduced tree cover, dominance of the herbaceous layer, and LUI are associated with less favourable conditions for diverse native communities. This pattern across the physiognomic gradient highlights the importance of maintaining structural complexity when interpreting variation in native understory diversity.

The contrasting associations of native and exotic species with livestock use documented here may have ecological implications beyond changes in species richness and diversity, including potential consequences for nutrient cycling, habitat structure for dependent fauna, and ecosystem resilience (Díaz et al. 2007; Arias Sepúlveda and Chillo 2017; Joelson et al. 2025). Global multitrophic syntheses have reported that reductions in plant diversity associated with livestock grazing are accompanied by declines in herbivore and pollinator communities (Filazzola et al. 2020), suggesting that the patterns observed in *A. chilensis* forests may also extend to other ecosystem components (Le Provost et al. 2022). Our results indicate that LUI was more consistently associated with changes in understory plant communities than with early regeneration establishment, reinforcing the value of evaluating multiple ecological indicators within a structural framework that accounts for contrasting forest structural conditions.

An important consideration is that forest physiognomy and LUI, although evaluated simultaneously, represent ecological processes operating at different temporal scales. Forest physiognomies reflect the cumulative outcome of stand development, disturbance history, and land use over decades, providing a relatively stable structural context (Oliver and Larson 1996; Burns et al. 2013). In contrast, the LUI estimated here captures livestock use over approximately one year prior to sampling, and may not fully represent the long-term grazing history of each stand. This temporal mismatch is a recognised limitation of cross-sectional studies in grazed ecosystems (Milchunas and Lauenroth 1993), where plant community responses often integrate grazing effects accumulated over multiple years or decades (Díaz et al. 2007). Nevertheless, long-standing silvopastoral use in northern Patagonian *A. chilensis* forests (Trinco et al. 2021) suggests that many sampled stands have experienced relatively persistent livestock use over time. Moreover, the physiognomic framework integrates the cumulative influence of stand development, disturbance history, timber harvesting, and long-term livestock use. Rather than representing the same ecological process, forest physiognomy and LUI were intended to capture complementary dimensions of forest dynamics: the long-term structural legacy of stand development and land use, and the recent intensity of livestock use. Interpreting both variables together therefore provides a broader ecological context than either measure alone.

4.2 Management implications of the physiognomy framework

The physiognomic framework proposed here provides a practical basis for integrating forest structure into management decisions in *A. chilensis* forests. Our results indicate that patterns of regeneration and understory composition were associated not only with livestock use intensity, but also with the structural context represented by forest physiognomy and, in the case of regeneration density, with interaction between the two. Consequently, management strategies may benefit from being adapted to the ecological characteristics and productive potential of each physiognomy rather than applying uniform grazing or silvicultural prescriptions. From this perspective, ecological restoration does not necessarily require livestock exclusion, but may instead rely on management practices aimed at maintaining or recovering desirable structural conditions while supporting ecosystem functioning and productive capacity (Messier and Puettmann 2011; Hobbs 2016; Hanisch and Pinotti 2024).

In closed forests, where both initial and advanced regeneration were generally present under low canopy openness, and where the association between LUI and regeneration density was weakest, silvicultural interventions that reduce competition while maintaining regeneration protection may be appropriate. Livestock grazing may remain compatible with these conditions provided that browsing impacts – which were associated with LUI across physiognomies – are monitored and shrub control does not compromise tree

recruitment. Such practices could facilitate sapling release above the browsing zone while maintaining both timber and forage production (Zerbe et al. 2023; Rodríguez et al. 2026), taking into account local site conditions and habitat suitability for *A. chilensis* (Oddi et al. 2022).

Open forests may offer favourable conditions for reconciling timber production, livestock use, and biodiversity conservation. Their intermediate structural complexity, together with the presence of both initial and advanced regeneration and relatively diverse understory communities, suggests that maintaining moderate canopy openness through low-intensity forestry combined with controlled grazing may help sustain both ecological and productive values, avoiding excessive canopy closure as suggested for other Patagonian forests (Rodríguez et al. 2026). Retaining seed trees, protecting regeneration, and promoting future crop trees (Cruz et al. 2018) may therefore represent appropriate management practices in these physiognomies, particularly for supporting decision-making at the farm scale.

In parkland environments, where tree regeneration is limited and the herbaceous matrix is dominant, management priorities may differ from those of more densely forested physiognomies. In these conditions, emphasis may be placed on maintaining soil stability, sustaining forage production, and controlling undesirable species that reduce grazing capacity. Where restoration of tree cover is an objective, active interventions such as planting, sapling protection, and temporary grazing exclusion may be required, although their feasibility will depend on previous land use, site conditions, and production objectives (Hobbs and Huenneke 1992; Carabelli et al. 2006; Nacif et al. 2023; Mundahl et al. 2025).

At the farm scale, the physiognomic framework may provide a spatial basis for planning silvicultural interventions, designing grazing rotations, and identifying areas for conservation or restoration (Garcia and Burns 2022; Varela et al. 2023; Pacini et al. 2024; Mackay-Smith et al. 2025). This is consistent with adaptive management, in which monitoring structural change over time informs adjustments to practices based on observed ecosystem responses (Lindenmayer et al. 2000; Varela et al. 2023). The proposed physiognomies may also help identify stands with contrasting silvicultural opportunities, guiding interventions such as thinning toward structural conditions that maintain forest resilience and multifunctionality, consistent with ecosystem-based silviculture approaches documented in other temperate forests (Messier and Puettmann 2011; Goldenberg et al. 2020; Guignabert et al. 2024; Uhl et al. 2025).

Our results provide partial support for the proposed hypotheses, revealing a more physiognomy-dependent pattern than initially expected. LUI was associated with probability of browsing damage and reduced sapling slenderness broadly across physiognomies. Regeneration density, however, was not associated with LUI as a uniform main effect but declined significantly with increasing LUI specifically in PR and UR physiognomies, indicating that physiognomy conditions where the association between LUI and regeneration density becomes detectable rather than acting independently of it. Native understory diversity and evenness declined consistently with LUI, whereas exotic species were more strongly associated with forest physiognomy. These findings indicate that forest physiognomy does not merely provide a static structural backdrop, but actively shapes where and how strongly livestock use is associated with regeneration and understory patterns, further supporting the value of the physiognomic framework for interpreting vegetation responses across heterogeneous forest conditions. Future work quantifying ecosystem services and structural thresholds across physiognomies would strengthen the framework's application to multifunctional management.

5 Conclusions

Associations between livestock use and ecological responses were not uniform, but depended on forest structural context: browsing damage probability and sapling morphological change were associated with livestock use broadly across physiognomies, whereas reductions in regeneration density were concentrated in the more structurally open physiognomies. Native understory richness, diversity, and evenness declined consistently with increasing livestock use. Exotic species diversity, in contrast, was more strongly associated with forest physiognomy, than with livestock use. These findings indicate that forest structural context determines not only the magnitude but also the detectability of associations between pastoral use and forest regeneration and understory communities.

Declarations

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Author Contribution

Conceptualization, N.B., M.A. and P.P.; methodology, N.B., M.A. and G.M.P.; software, N.B.; validation, N.B., M.A., P.P., M.B. and G.M.P.; formal analysis, N.B.; investigation, N.B., O.C.P. and A.P.B.; resources, M.A. and P.P.; data curation, N.B. and A.P.B.; writing—original draft preparation, N.B.; writing—review and editing, N.B., M.A., P.P., M.B., G.M.P.; visualization, N.B. and O.C.P.; supervision, M.A., P.P. and M.B.; project administration, N.B. and M.A.; funding acquisition, M.A. and N.B. All authors have read and agreed to the published version of the manuscript.

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Data Availability

The datasets generated and analyzed during this study are not publicly available because they form part of an ongoing research project but are available from the corresponding author upon reasonable request.

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Figures

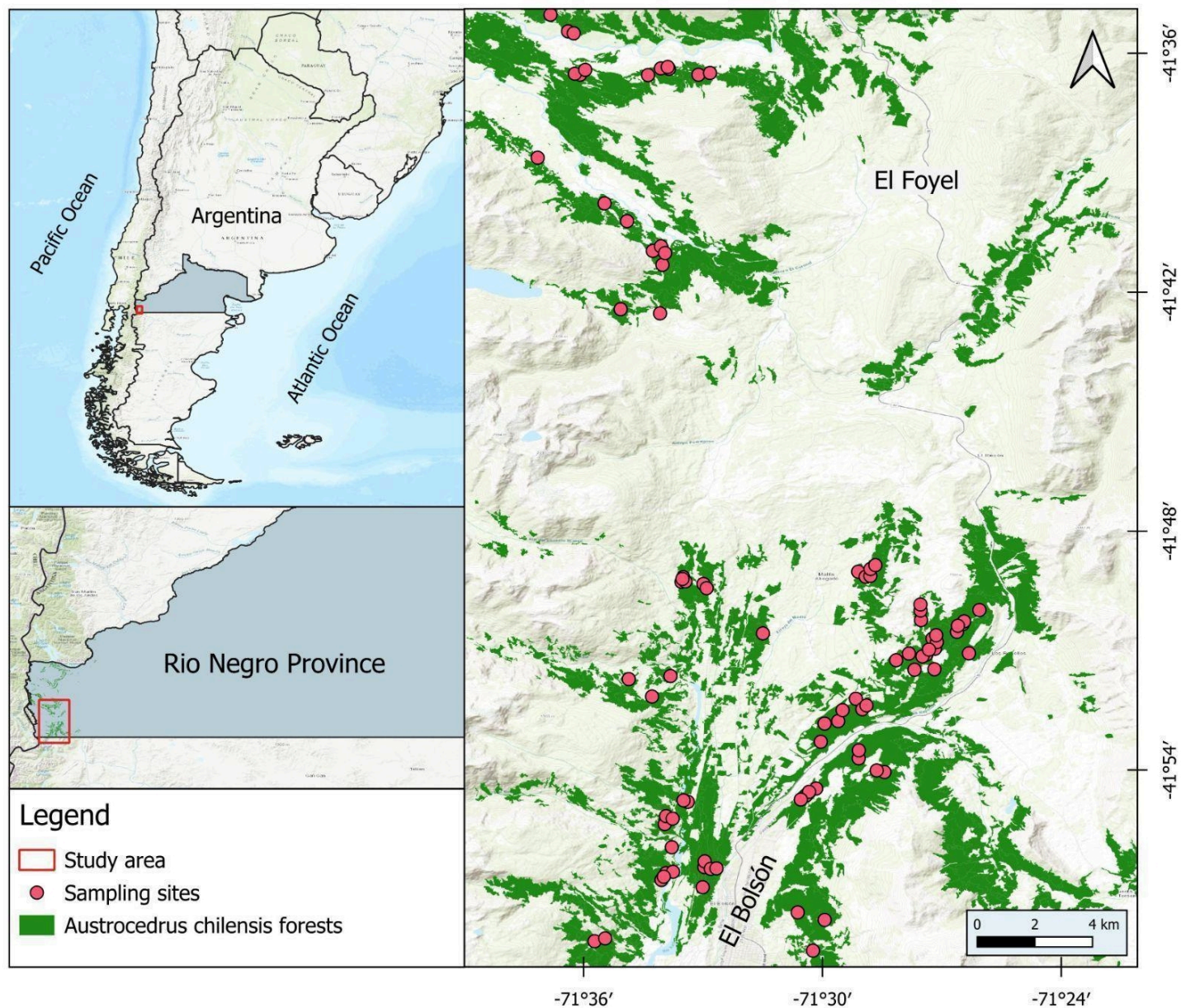


Figure 1

Sampling stands (red dots, $n = 95$) in *Austrocedrus chilensis* forests (green cover) of northern Patagonia (Argentina).

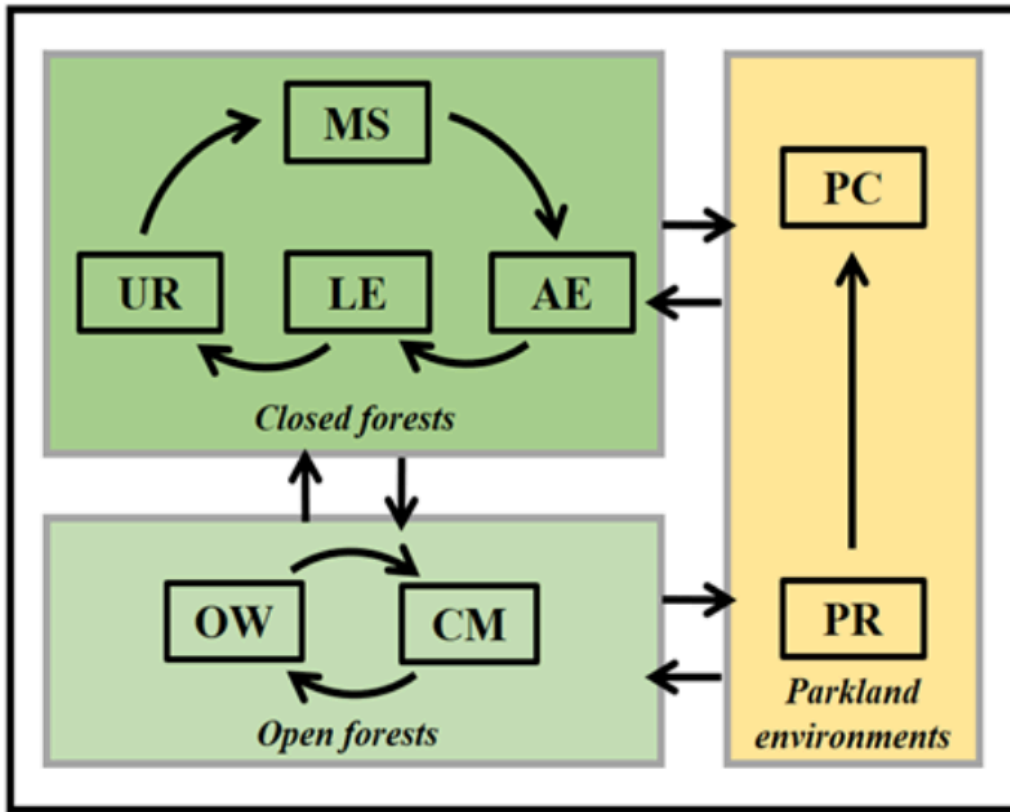


Figure 2

Conceptual diagram representing the physiognomic framework identified in *Austrocedrus chilensis* forests and their potential trajectories. Green boxes represent forests physiognomies, both closed and open forests, whereas yellow boxes represent parklands environments associated with intensive use and strong canopy opening. MS = maximum stand occupancy, LE = late stem exclusion, AE = active stem exclusion, UR = understory reinitiation, OW = open woodland, CM = cohort mixing, PR = parkland remnant, PC = pastoral clearing.

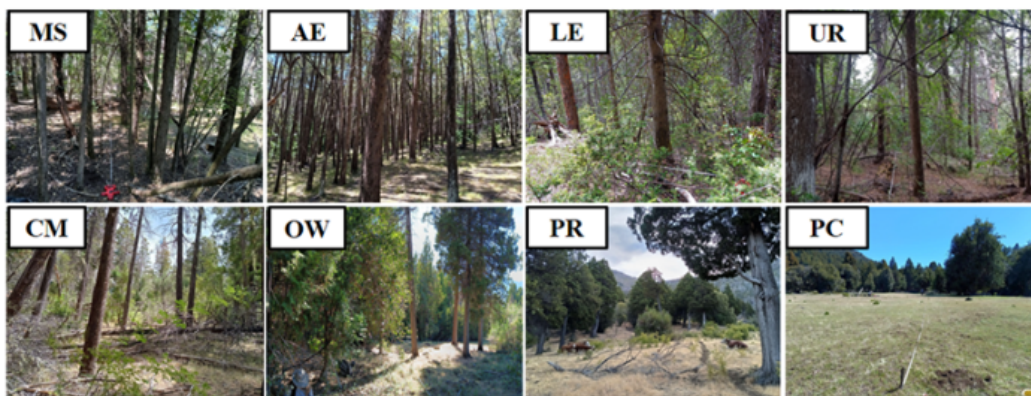


Figure 3

Representative field photographs of the eight forest physiognomies identified in *Austrocedrus chilensis* forests. MS: Maximum stand occupancy; AE: Active stem exclusion; LE: Late stem exclusion; UR: Understory reinitiation; CM: Cohort mixing; OW: Open woodland; PR: Parkland remnant; PC: Pastoral clearing. Photographs illustrate the contrasting structural conditions encompassed by the physiognomic framework, ranging from dense closed-canopy forests to open woodland and parkland environments.

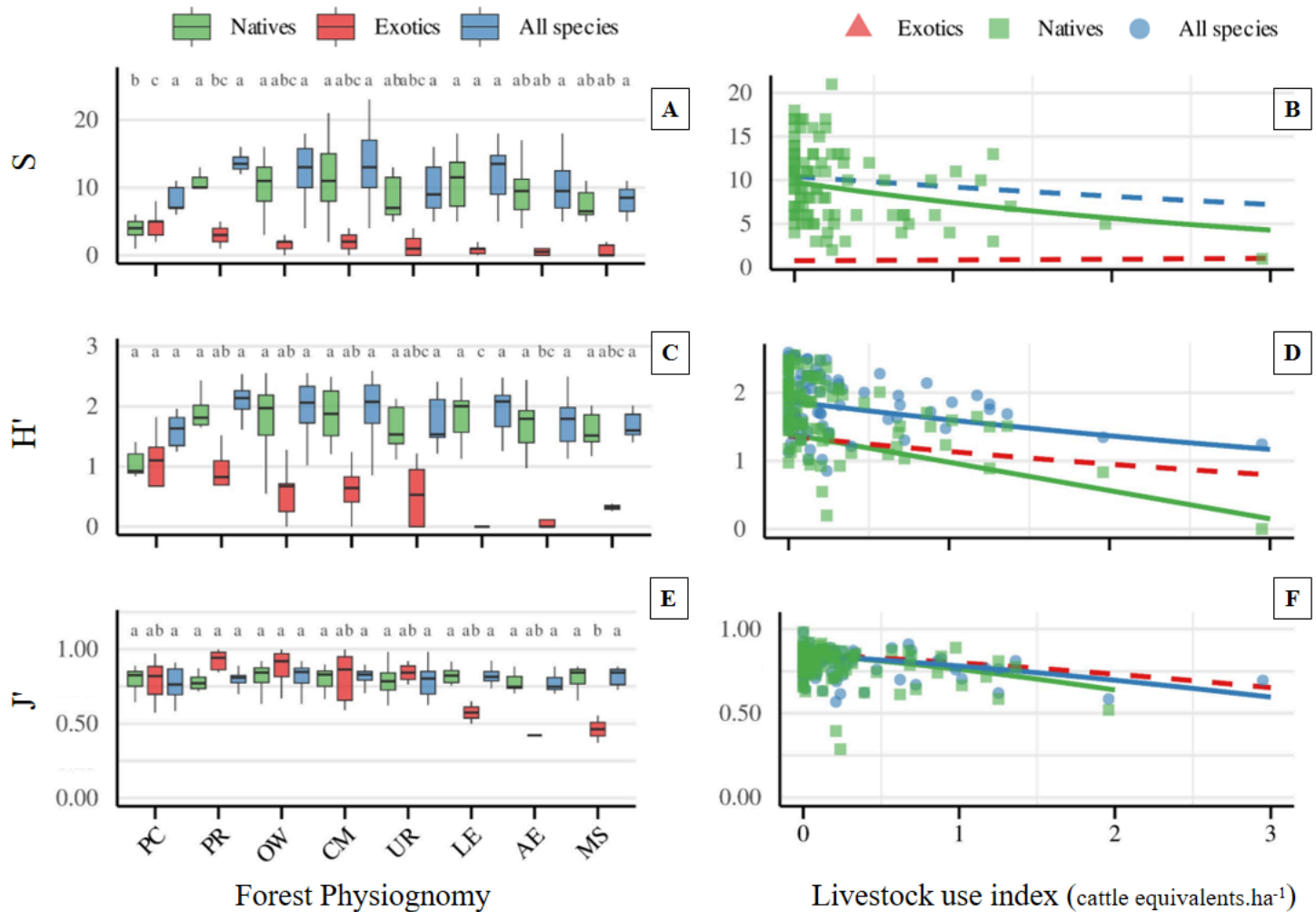


Figure 4

Effects of forest physiognomy (A, C, E) and livestock use index (B, D, F) on understory plant diversity in *Austrocedrus chilensis* stands (n = 95). Diversity metrics include species richness (S, A, B), Shannon diversity (H', C, D), and Pielou's evenness (J', E, F), for all species (blue), native species (green), and exotic species (red). Different letters indicate significant differences among physiognomies (p < 0.05). Right panels show fitted relationships with 95% confidence intervals. Solid lines indicate significant associations with LUI (p < 0.05), whereas dashed lines indicate non-significant relationships. Physiognomy acronyms: MS = maximum stand occupancy, LE = late stem exclusion, AE = active stem exclusion, UR = understory reinitiation, OW = open woodland, CM = cohort mixing, PR = parkland remnant, PC = pastoral clearing.

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