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Drivers of honeybee forage supply across contrasting land covers in forested Patagonia

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Abstract

The forested regions of Patagonia host some of the southernmost honeybee (*Apis mellifera*) apiaries in the world, where beekeeping shares the same vegetation matrix with livestock farming. We evaluated how environmental drivers (e.g., precipitation, temperature, elevation) and drivers associated with vegetation structure and use (e.g., canopy cover, ground cover, and grazing pressure) relate to the taxonomic composition, origin, life form, and phenology of bee forage supply in deciduous forests, evergreen forests, and open areas of the Aysén Region, Chile (44–49ºS). We used 363 plots (~ 1 ha) near the main apiaries and quantified the biomass, richness, and native and exotic proportions of the supply provided by 55 species of apicultural interest. Data were analysed with univariate (e.g., generalised linear mixed models) and multivariate methods (e.g., PERMANOVA, db-RDA, variance partitioning). The composition of bee forage supply differed among land covers (PERMANOVA, R^2 = 0.085; p = 0.001). Drivers explained 15.2% of compositional variation (db-RDA, adjusted R^2; p = 0.001). Vegetation structure and use independently explained 10.0% of compositional variation, compared with 3.6% for environmental drivers (both p = 0.001), with stand structure accounting for the largest independent fraction (4.3%). Higher canopy cover was associated with a lower proportion of exotic species in the supply (= -0.86; p < 0.001), and grazing pressure with a higher proportion (= 0.26; p = 0.001). Life-form and phenological composition also differed among covers (PERMANOVA, R^2 = 0.112 and 0.076, respectively; p = 0.001). In forests, the supply was concentrated in peak growth, and woody species contributed about half of it. Herbs accounted for 91% of the supply in open areas, where the share flowering during senescence was larger than in forests. These results suggest that part of the potential bee forage supply is linked to factors that land management can modify. Maintaining canopy cover in native forests may help sustain the bee forage supply provided by native species.

1. Introduction

The western honeybee (*Apis mellifera* Linnaeus, 1758) is the main managed pollinator worldwide and supports economically important beekeeping activities (Klein et al., 2007; Gallai et al., 2009). Its diet depends on the surrounding vegetation, from which it obtains nectar as an energy source and pollen as a protein source (Crane, 1990; Cannizzaro et al., 2022). In Patagonia, forested regions host some of the southernmost *A. mellifera* apiaries in the world (Molina et al., 2016). At this geographical extreme, the floral resources provided to honeybees by plants of apicultural interest (hereafter, bee forage supply) vary along climatic gradients and across contrasting land covers (de Groot et al., 2023; Salinas Sanhueza and Silva Labbé, 2025). This variation provides an opportunity to examine how environmental gradients and vegetation use relate to the composition and availability of floral resources for pollinators (Barahona et al., 2024; Birkenbach et al., 2024).

Melissopalynological studies in Patagonia have shown that the diet of *A. mellifera* includes both native and exotic species (Forcone et al., 2009; de Groot et al., 2023). Cattle (*Bos taurus*) and sheep (*Ovis aries*) farming can modify the composition and structure of vegetation through biomass removal and changes in diversity, and is associated with reduced canopy cover (Salinas et al., 2017; Rusch and Varela, 2019;

Huertas Herrera et al., 2023; Salinas, 2024). This coexistence under a land-sharing model (Phalan et al., 2011) can generate indirect interactions, because both productive activities depend on the same vegetation base (de Groot et al., 2023; Huertas Herrera et al., 2024; Salinas Sanhueza and Silva Labbé, 2025).

Grazing-related changes in vegetation can shape plant community assembly (Funk, 2021; De Wit, 2025). Grazing pressure and canopy cover have been shown to alter floristic composition (Quinteros et al., 2010, 2017), and grazing can favour the spread of exotic herbs in disturbed environments (Sánchez-Jardón et al., 2014). These relationships raise the question of whether variation in bee forage supply is more closely related to environmental drivers or to drivers associated with vegetation structure and use.

This study aims to analyse how environmental drivers (e.g., precipitation, temperature, elevation) and drivers associated with vegetation structure and use (e.g., canopy cover, ground cover, and grazing pressure) relate to the taxonomic composition, origin, life form, and phenology of bee forage supply in three contrasting land covers of Chilean Patagonia: deciduous forests, evergreen forests, and open areas. We addressed the following questions: (i) How do the biomass, richness, and composition of bee forage supply vary among land covers? (ii) What is the relative contribution of environmental drivers and vegetation structure and use to the variation in the composition of bee forage supply? (iii) How do native and exotic species respond to the gradients of these drivers? (iv) How does bee forage supply vary among land covers in terms of life form and flowering phenological phase?

2. Methods

2.1 Study area

The study was conducted in the Aysén Region, Chilean Patagonia, between 44º and 49ºS (Fig. 1). The climate is temperate and varies with location and elevation (AGRIMED, 2017). Annual precipitation ranges from ~ 3,000 to ~ 4,000 mm in humid sectors and decreases to ~ 500 mm in drier areas. Summer temperatures range from 10 to 18 ºC, and winter temperatures drop below 0 ºC. The landscape comprises evergreen and deciduous forests, as well as open areas mainly associated with grasslands used for livestock (Huertas Herrera et al., 2023). Forests comprise tree species from several families, including Nothofagaceae (e.g., *Nothofagus antarctica*, *N. pumilio*, *N. betuloides*, and *N. dombeyi*), Myrtaceae (e.g., *Amomyrtus luma* and *Luma apiculata*), Podocarpaceae (*Saxegothaea conspicua* and *Podocarpus nubigena*), Atherospermataceae (*Laureliopsis philippiana*), and Winteraceae (*Drimys winteri*), among others (Huertas Herrera et al., 2023).

In the early twentieth century, extensive areas were burned to expand land available for livestock grazing, mainly cattle and sheep (Veblen et al., 2003; Veblen, 2007). This created open environments and favoured the establishment of forage species (Veblen and Lorenz, 1988; Mundo et al., 2017). As a result, the current landscape forms a mosaic of deciduous forests, evergreen forests, and open areas where livestock farming and beekeeping coexist (Salinas, 2024; Salinas Sanhueza and Silva Labbé, 2025).

Beekeeping is an emerging economic activity, with about one hundred beekeepers and more than one thousand hives, concentrated mainly in areas dominated by grasslands and native forests (Salinas Sanhueza and Silva Labbé, 2025).

2.2 Sampling design

We established a stratified random sampling design along an extensive latitudinal gradient that includes the foraging areas (~ 5 km) of the main apiaries (Fig. 1). We analysed 363 plots (~ 1 ha each) where species of apicultural interest were present. To represent the contrasting land covers of the landscape, plots were classified into three land covers: (i) deciduous forest (n = 216), represented by deciduous stands (e.g., *N. pumilio* and *N. antarctica*); (ii) evergreen forest (n = 49), characterised by evergreen stands (e.g., *N. dombeyi*, *N. betuloides*, *L. philippiana*, and *D. winteri*), and (iii) open areas (n = 98), corresponding to grasslands.

Forest structure was characterised along two 50-m transects randomly laid out from the centre of each plot. Using point sampling (basal area factor, BAF 4 m^2 ha^{-1}) with a digital clinometer (Haglöf EC II D-R), the diameter at breast height (DBH) of each selected tree was measured with a calliper and its development phase was recorded (initial or final growth, mature, or collapse; Schmidt and Urzúa, 1982). Basal area (BA) was derived from point sampling, and dominant height (HD) was measured with a laser hypsometer (TruPulse® 200L). Regeneration and dead wood on the ground (DW; branches and logs in three size classes of < 5, 5 to 10, and > 10 cm) were recorded in two 2 × 5 m strips per transect. Canopy cover (CC) was estimated from hemispherical photographs taken at ground level with an 8-mm fisheye lens (Sigma) mounted on a 35-mm digital camera (Nikon) levelled on a tripod. Grazing pressure (GP) was estimated with an index based on standardised counts of domestic herbivore dung (e.g., cattle and sheep) in the plot, which was transformed into a percentile (0-100) for modelling. Ground cover was recorded by point intercept along the same transects, as the percentage of points falling on litter (LIT), bare soil (BARE), non-vascular organisms (NV; e.g., mosses, lichens, fungi), rock outcrop (ROCK), exposed roots (ROOT), and livestock dung (DUNG).

Plant community characteristics were assessed by recording vascular plant richness (number of species of ferns, gymnosperms, and angiosperms) in each plot, and plant cover (%) was estimated using the modified Braun-Blanquet scale (Clarke, 1986; Lencinas et al., 2024). To analyse bee forage supply, we estimated the biomass (kg ha^{-1}) of a functional subset of 55 vascular plant species catalogued as being of regional apicultural interest for their contribution of nectar, pollen, or both (de Groot et al., 2023; Salinas Sanhueza and Silva Labbé, 2025). Here, this biomass was used as a proxy for the potential supply of floral resources. Samples were collected destructively from two randomly placed 0.5-m^2 quadrats per plot (1 m^2 in total). All plant material inside each quadrat was cut at ground level, taken to the laboratory, oven-dried at 60 ºC (Binder, Tuttlingen, Germany) to constant weight, and weighed on an analytical balance (± 0.0001 g; Boeco, Hamburg, Germany). Bee forage species were classified by origin (native or exotic) and main life form (tree, shrub, herb, or liana), following Dale et al. (2002) and Faber-Langendoen et al. (2014).

The temporal dimension of bee forage supply was assessed based on the flowering months of the 55 species of apicultural interest (de Groot et al., 2023; Salinas Sanhueza and Silva Labbé, 2025), using regional censuses and records, including specific studies for *Nothofagus* (Toro-Manríquez et al., 2016, 2022). Following a functional approach, species were then classified by calculating the proportion of their flowering that fell into the three dominant physiological phases of the agroclimatic curve of Patagonian vegetation (AGRIMED, 2017; Hepp, 2019): (i) peak growth (September to December, spring), synchronised with soil water availability and maximum biomass accumulation; (ii) senescence (January to March, summer), when strategies of tolerance to summer water deficit predominate; and (iii) dormancy (April to August, autumn and winter), marked by the winter temperature decline and vegetative arrest.

Abiotic gradients were characterised using climatic variables extracted from the WorldClim version 2.1 database (www.worldclim.org; Fick and Hijmans, 2017), including the maximum summer temperature (TMAX), the minimum winter temperature (TMIN), and the mean annual precipitation (PP). Topographic variables, namely elevation (ELEV), slope (SLOPE), hillshade (HS), and the east-west (EW) and north-south (NS) components of aspect, were derived from the SRTM digital elevation model (Farr et al., 2007). Spatial processing was performed in ArcMap 10.8 (ESRI, www.esri.com). Details of the variables representing environmental drivers and drivers associated with vegetation structure and use are presented in Table A1.

2.3 Data analysis

Bee forage supply was quantified at plot level through its biomass (kg ha^{-1}), the proportion of biomass contributed by native and exotic species, and richness (number of species).

Drivers were selected from the 29 candidate variables in Table A1. The association of each candidate with the composition of bee forage supply was assessed by fitting vectors to a principal coordinates ordination based on Bray-Curtis distance (envfit function, 999 permutations; Table A1). Drivers were then selected by forward selection in distance-based redundancy analysis (db-RDA; Legendre and Anderson, 1999) using the double stopping criterion of Blanchet et al. (2008), with a significance level of 0.05 corrected for the number of candidates (Bonferroni, $\alpha = 0.0017$; 4999 permutations) and the adjusted R^2 of the model with all candidates. At each step, only candidates that kept the variance inflation factor (VIF) of all selected drivers below 5 were considered (car package; Fox and Weisberg, 2019). ELEV was then tested conditional on the selected drivers, without the VIF constraint, and added if significant at the same level.

The effect of the retained drivers on bee forage supply variables was evaluated with generalised linear mixed models (GLMMs) using the glmmTMB package version 1.1.14 (Brooks et al., 2017; McGillycuddy et al., 2025). To account for the spatial structure of sampling, the 363 plots were grouped into 25 spatial sampling blocks covering sectors near apiaries and peripheral areas, which were included as a random effect in all models. Predictors were standardised (mean 0, standard deviation 1) before fitting, so coefficients (□) were comparable among drivers. We used a Tweedie distribution for bee forage biomass

(Dunn and Smyth, 2005), a Poisson distribution for species richness, and an ordered beta regression for the proportion of exotic species in the supply (Kubinec, 2023), whose complement is the proportion of native species. Model assumptions and residual dispersion were checked with simulations using the DHARMa package (Hartig, 2026). Differences in bee forage biomass and richness among the three land covers were evaluated with GLMMs including land cover as a fixed effect, followed by pairwise comparisons of estimated marginal means (Tukey adjustment) with the emmeans package (Lenth and Piaskowski, 2026). The marginal and conditional R^2 of each model were estimated with the performance package (Lüdecke et al., 2021).

We used multivariate analyses to examine variation in the taxonomic composition of bee forage supply based on the biomass matrix of the 55 species through permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001) with Bray-Curtis distance and 999 permutations. The direction of the relationships between the retained drivers and composition was visualised with db-RDA. To quantify the relative contribution of drivers, we performed variance partitioning (partial db-RDA; Borcard et al., 1992), first with two blocks, namely environmental drivers (TMAX, TMIN, and ELEV) and vegetation structure and use (CC, BA, HD, LIT, BARE, NV, and GP), and then with the latter partitioned into stand structure (CC, BA, and HD), ground cover (LIT, BARE, and NV), and grazing pressure (GP). For each block, we reported its independent fraction (adjusted R^2). The affinity of species for each of the three land covers was represented with a ternary diagram showing the proportion of their biomass contributed by each cover. Species were ordered according to their flowering profile through a principal coordinates analysis with Euclidean distance (PCoA; Gower, 1966). Multivariate analyses were performed with the vegan package version 2.7-5 (Oksanen et al., 2026).

Life form composition and phenological composition of the supply were compared among the three land covers with PERMANOVA, using biomass matrices aggregated by life form and by phenological phase, respectively. For the phenological analysis, the biomass of each species was distributed among phases in proportion to its flowering months. The main phenological phase of each species was assigned based on the proportion of documented flowering months falling within each phase of the regional agroclimatic curve (Hepp, 2019), with ties assigned to the earlier phase. All statistical analyses and graphics were performed in RStudio (www.rstudio.com) as an interface to the R statistical environment (www.r-project.org; R Core Team, 2026).

3. Results

3.1 Variation in bee forage supply among land covers

The composition of bee forage supply differed among the three land covers (PERMANOVA, R^2 = 0.085; F = 16.7; p = 0.001; Figure 2). In evergreen forest, bee forage supply consisted almost exclusively of native species, mostly woody (e.g., *N. dombeyi*, *Fuchsia magellanica*). In deciduous forest, it combined native woody species (e.g., *N. pumilio*, *Berberis microphylla*) with herbs, including exotic ones (e.g., *Taraxacum officinale*). In open areas, it consisted mainly of exotic herbs (e.g., *Trifolium pratense*, *T. repens*). A subset

of species was more evenly distributed among covers and was located towards the centre of the diagram. Bee forage biomass differed among the three covers. It was highest in open areas (15.2 ± 1.5 kg ha^{-1}; estimated mean ± SE), intermediate in deciduous forest (10.3 ± 0.8 kg ha^{-1}), and lowest in evergreen forest (6.6 ± 0.8 kg ha^{-1}; $p < 0.001$ for all comparisons). Richness was similar among covers, except for lower richness in evergreen forest (3.5 ± 0.4 species per plot) than in open areas (4.4 ± 0.4; $p = 0.039$).

3.2 Contribution of environmental drivers and vegetation structure and use

Forward selection retained nine of the 29 candidate drivers (Table 1). CC entered first and made the largest contribution to compositional variation (increase in adjusted $R^2 = 0.065$), followed by TMAX (0.027) and TMIN (0.019). Three ground-cover variables (LIT, NV, and BARE), two further stand-structure variables (HD and BA), and GP made smaller contributions (0.004 to 0.009 each). The maximum VIF of the nine selected drivers was 4.6. ELEV was also significant given the nine selected drivers ($F = 2.9$; $p = 0.001$) and was added as a tenth driver, although it was collinear with TMIN (Spearman $\rho = -0.81$; maximum VIF = 8.8, for TMIN). Together, the ten drivers explained 15.2% of compositional variation (db-RDA, adjusted R^2; $F = 7.5$; $p = 0.001$; Figure 3A).

Variance partitioning showed that vegetation structure and use independently explained 10.0% of compositional variation, and environmental drivers (TMAX, TMIN, and ELEV) accounted for 3.6% (both $p = 0.001$). Within vegetation structure and use, stand structure (CC, BA, and HD) had the largest independent fraction (4.3%), followed by ground cover (LIT, BARE, and NV; 2.4%) and grazing pressure (GP; 0.4%; all $p = 0.001$).

Table 1. Drivers of the composition of bee forage supply and their contribution to explained variation. R^2adj, cumulative adjusted R^2; ΔR^2adj, increase in adjusted R^2; F, pseudo-F; p, permutation-based probability. Candidate variables are listed in Table A1.

Driver	Unit	R^2adj	ΔR^2adj	F	p
Canopy cover	%	0.065	0.065	26.3	0.001
Maximum summer temperature	ºC	0.092	0.027	11.8	0.001
Minimum winter temperature	ºC	0.111	0.019	8.8	0.001
Litter	% cover	0.121	0.009	4.8	0.001
Non-vascular cover	% cover	0.127	0.006	3.6	0.001
Dominant height	m	0.133	0.006	3.5	0.001
Bare soil	% cover	0.139	0.005	3.3	0.001
Basal area	$m2\ ha^{-1}$	0.143	0.005	3.0	0.001
Grazing pressure	percentile 0 to 100	0.147	0.004	2.6	0.001
Elevation	m a.s.l.	0.152	0.005	2.9	0.001

3.3 Responses of native and exotic species

GLMMs showed that CC was the driver most consistently associated with bee forage biomass and the proportion of exotic species (Table 2). CC was positively associated with native bee forage biomass (kg ha^{-1}; standardised coefficient = 0.66; $p < 0.001$) and negatively associated with the biomass (= -0.56; $p < 0.001$) and proportion of exotic species in the bee forage supply (= -0.86; $p < 0.001$).

Table 2. Associations between drivers and bee forage supply, expressed as standardised coefficients () from the GLMMs. CC, canopy cover; TMAX, maximum summer temperature; TMIN, minimum winter temperature; LIT, litter; NV, non-vascular cover; HD, dominant height; BARE, bare soil; BA, basal area; GP, grazing pressure; ELEV, elevation; R^2m, marginal R^2; R^2c, conditional R^2. *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$.

Driver	Exotic proportion (0-1)	Exotic biomass (kg ha^{-1})	Native biomass (kg ha^{-1})	Bee forage richness
CC	-0.86***	-0.56***	+0.66***	+0.04
TMAX	+0.04	+0.16	+0.13	+0.04
TMIN	0.00	-0.08	-0.13	-0.04
LIT	-0.10	-0.25**	-0.09	-0.01
NV	-0.25*	-0.32***	+0.08	-0.04
HD	+0.08	+0.16	-0.30**	-0.11*
BARE	-0.09	-0.08	+0.07	+0.03
BA	+0.02	-0.07	+0.13	0.00
GP	+0.26**	+0.11	-0.07	+0.03
ELEV	-0.33	-0.34*	+0.06	-0.10
R^2m	0.52	0.39	0.27	0.11
R^2c	0.89	0.78	0.48	0.29

GP was associated with a higher proportion of exotic species in the bee forage supply (= 0.26; p = 0.001). NV was associated with a lower proportion (= -0.25; p = 0.014) and biomass of exotic species (= -0.32; p < 0.001), and LIT (= -0.25; p = 0.008) and ELEV (= -0.34; p = 0.026) with lower exotic biomass. ELEV and TMIN were collinear, and neither was significantly associated with the exotic proportion (ELEV, = -0.33; p = 0.052; TMIN, = 0.00; p = 0.996). HD was associated with lower native biomass (= -0.30; p = 0.005) and lower bee forage richness (= -0.11; p = 0.040), and richness showed no significant relationship with the other drivers. TMAX, TMIN, BARE, and BA showed no significant relationship with any response variable (Table 2).

3.4 Changes in supply by life form and phenology

Life-form composition of bee forage supply differed among land covers (PERMANOVA, R^2 = 0.112; F = 22.7; p = 0.001). In deciduous and evergreen forests, the supply combined woody species (trees and shrubs; 47.6% and 54.1%, respectively) and understorey herbs (51.9% and 44.5%). By contrast, herbs accounted for 90.7% of the supply in open areas.

The phenological composition of bee forage supply also differed among land covers (PERMANOVA, R^2 = 0.076; F = 14.7; p = 0.001). In deciduous and evergreen forests, the largest share of the supply corresponded to peak growth (September to December; 58.8% and 57.8%, respectively), mostly from trees and shrubs (e.g., *N. pumilio*, *B. microphylla*). In open areas, the supply was split between peak growth (42.3%) and senescence (January to March; 42.1%), with a larger contribution of senescence

than in forests (31.4% and 34.4%), mostly from exotic herbs (e.g., *T. pratense*, *Hypochaeris radicata*; Figure 3B).

4. Discussion

4.1. Variation in bee forage supply among land covers

The forested regions of Patagonia form a landscape characterised by a mosaic of forests and open areas that vary in structure and composition along temperature, precipitation, and elevation gradients (Veblen et al., 2003; Veblen, 2007). Our results show that the composition of bee forage supply is associated with these land covers. As shown in Fig. 2, species show partial taxonomic and functional differentiation among covers. These differences indicate a turnover in the taxonomic composition of bee forage supply among land covers (de Groot et al., 2023; Salinas Sanhueza and Silva Labbé, 2025).

4.2. Associations with environmental drivers and vegetation structure and use

Vegetation structure and use independently explained a larger proportion of the variation in the composition of bee forage supply than environmental drivers, with stand structure as the main block. The lower proportion of exotic bee forage under higher CC agrees with the greater representation of exotic herbs under lower canopy cover in grazed Patagonian systems (Sánchez-Jardón et al., 2014; Alonso et al., 2020). After accounting for CC and the other drivers, taller stands were associated with less native bee forage biomass and fewer bee forage species, consistent with changes in understorey composition along forest structure gradients (Quinteros et al., 2010). Ground cover added information not captured by stand structure. Plots with higher NV and LIT had lower exotic biomass, which may reflect shaded and humid forest floors that are less favourable to exotic herbs. By contrast, GP was associated with a higher proportion of exotic bee forage, a pattern commonly reported in environments disturbed by livestock (Bahamonde et al., 2013; Salinas, 2021; Birkenbach et al., 2024). Exotic bee forage biomass decreased with elevation, although the strong correlation between elevation and minimum winter temperature prevented these effects from being separated. These results suggest that the composition of bee forage supply is jointly associated with environmental drivers and with vegetation structure and use, with a greater independent contribution of the latter in our models.

4.3. Functional and phenological changes in bee forage supply

Land cover was associated with differences in the composition and seasonality of bee forage supply. Forests and open areas differed in dominant life forms and in the temporal distribution of the supply (Fig. 3). In forests, the supply of native woody species was concentrated in peak growth. By contrast, in open areas, herbs, mostly exotic, contributed a larger share of the supply during senescence (January to March) than in forests. This pattern is consistent with observations in open and grazed environments, where herbs may concentrate their flowering later in the season (Tadey, 2020).

The heterogeneity among land covers suggests a possible spatial and temporal complementarity in the availability of floral resources for honeybees at the landscape scale, whereby the forest supply during peak growth is complemented by that of open areas during senescence (de Groot et al., 2023; Birkenbach et al., 2024; Salinas Sanhueza and Silva Labbé, 2025).

4.4. Implications

Our results identify land management as a relevant component for maintaining bee forage supply in areas where livestock farming and beekeeping coexist. These findings have three practical implications for managing apicultural resources: (i) conserving forest structure may maintain a supply composition associated with native species, and its protection and enrichment with native bee forage species is a management option to be evaluated; (ii) reduced canopy cover, the loss of litter and non-vascular ground cover, and intensified grazing may be associated with a greater representation of exotic species in the potential bee forage supply; and (iii) land-cover heterogeneity generates temporal differences in supply composition, suggesting a possible spatial and temporal complementarity between forests and open areas.

This study has limitations that guide the interpretation of its results. (i) We did not evaluate whether the different covers coexist within the foraging radius of each apiary, a necessary condition for the temporal complementarity described here to operate without migratory beekeeping. (ii) Some species of apicultural value reported for Patagonia (e.g., *Weinmannia trichosperma*, *Caldcluvia paniculata*) were not recorded in the plots, so their contribution to the supply could not be assessed. (iii) The biomass of species of apicultural interest is an indicator of potential supply and does not quantify floral display or nectar and pollen production. Future studies should quantify the nectar and pollen contribution of each species according to its abundance and period of availability.

5. Conclusion

Across the contrasting land covers studied, the composition of bee forage supply was more closely associated with vegetation structure and use than with environmental drivers. This suggests that part of the potential bee forage supply is linked to factors that land management can modify. Canopy cover showed the strongest and most consistent associations, and grazing pressure was associated with a higher proportion of exotic species. Forests supported a supply with a greater share of native woody species, concentrated in peak growth, whereas open areas supported a supply dominated by exotic herbs, with a larger share flowering during senescence. Because forests and open areas differ in the timing of their supply, land-cover heterogeneity could extend the availability of floral resources for honeybees across the season, if both land covers lie within the foraging radius of the same apiary. Bee forage supply could therefore be explicitly incorporated into land management in areas where livestock farming and beekeeping coexist. Maintaining canopy cover in native forests may help sustain the bee forage supply provided by native species.

Declarations

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Data availability

All available data and materials are included in the manuscript.

Declaration of generative AI and AI-assisted technologies

During the preparation of this work, the authors used Claude Opus 5.5 (Anthropic) to edit the English language and improve the clarity of the text, and Scopus AI (Elsevier) to support the literature search. After using these tools, the authors reviewed and edited the content as needed and take full responsibility for the content of the published article.

Author Contribution

JSS: Writing - original draft, Writing - review and editing. AHH: Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Writing - original draft, Writing - review and editing. MTM: Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Writing - review and editing. SVC: Data curation. FSL: Writing - review and editing.

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Figures

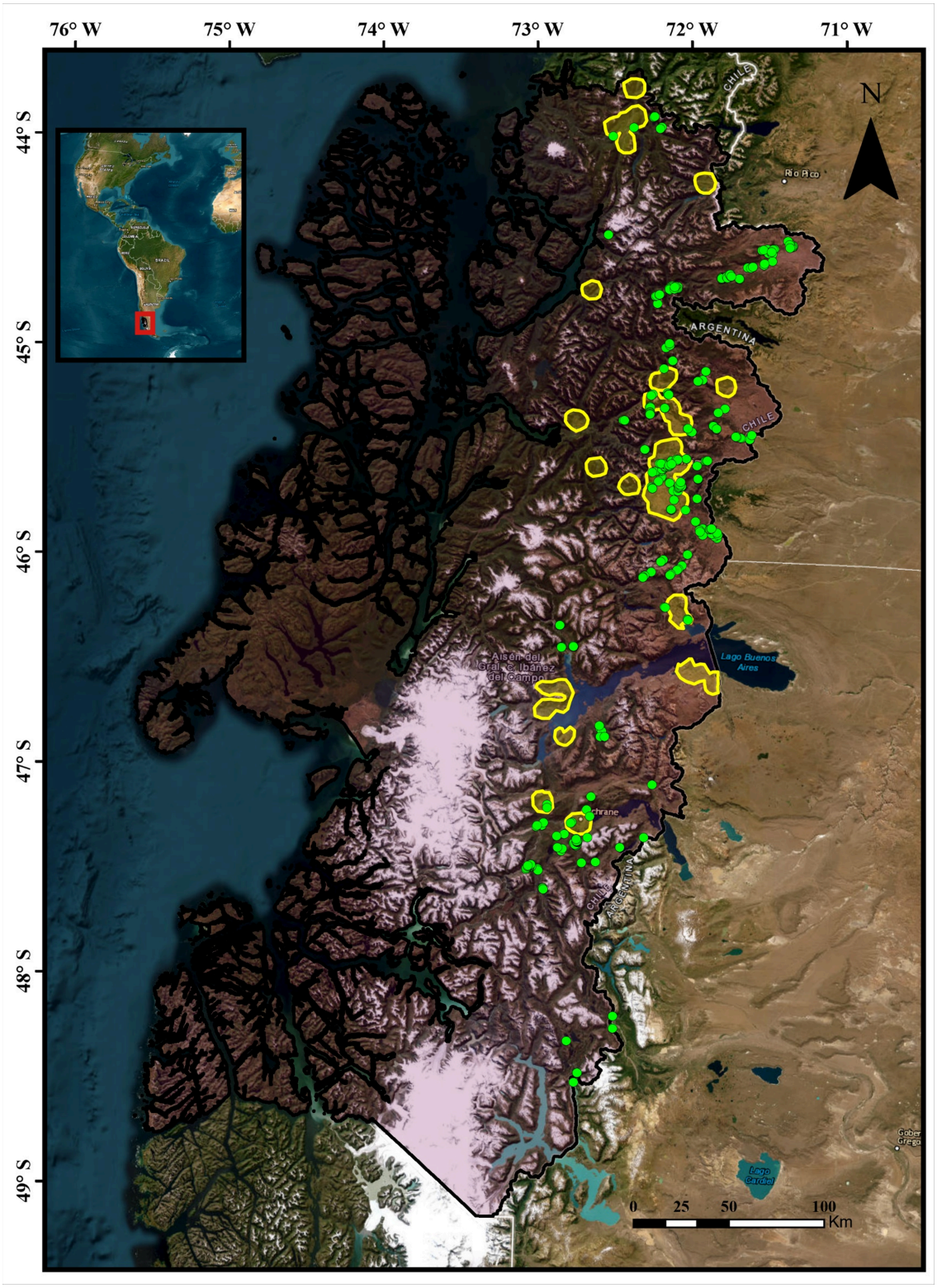


Figure 1

Study area. Green dots indicate the network of sampling plots; polygons with yellow outlines delimit the foraging area of the main apiaries (Salinas Sanhueza and Silva Labbé, 2025). The inset shows the

location of the study area (red rectangle) in South America. Basemap source: ESRI ArcGIS software (ArcMap 10.8; www.esri.com).

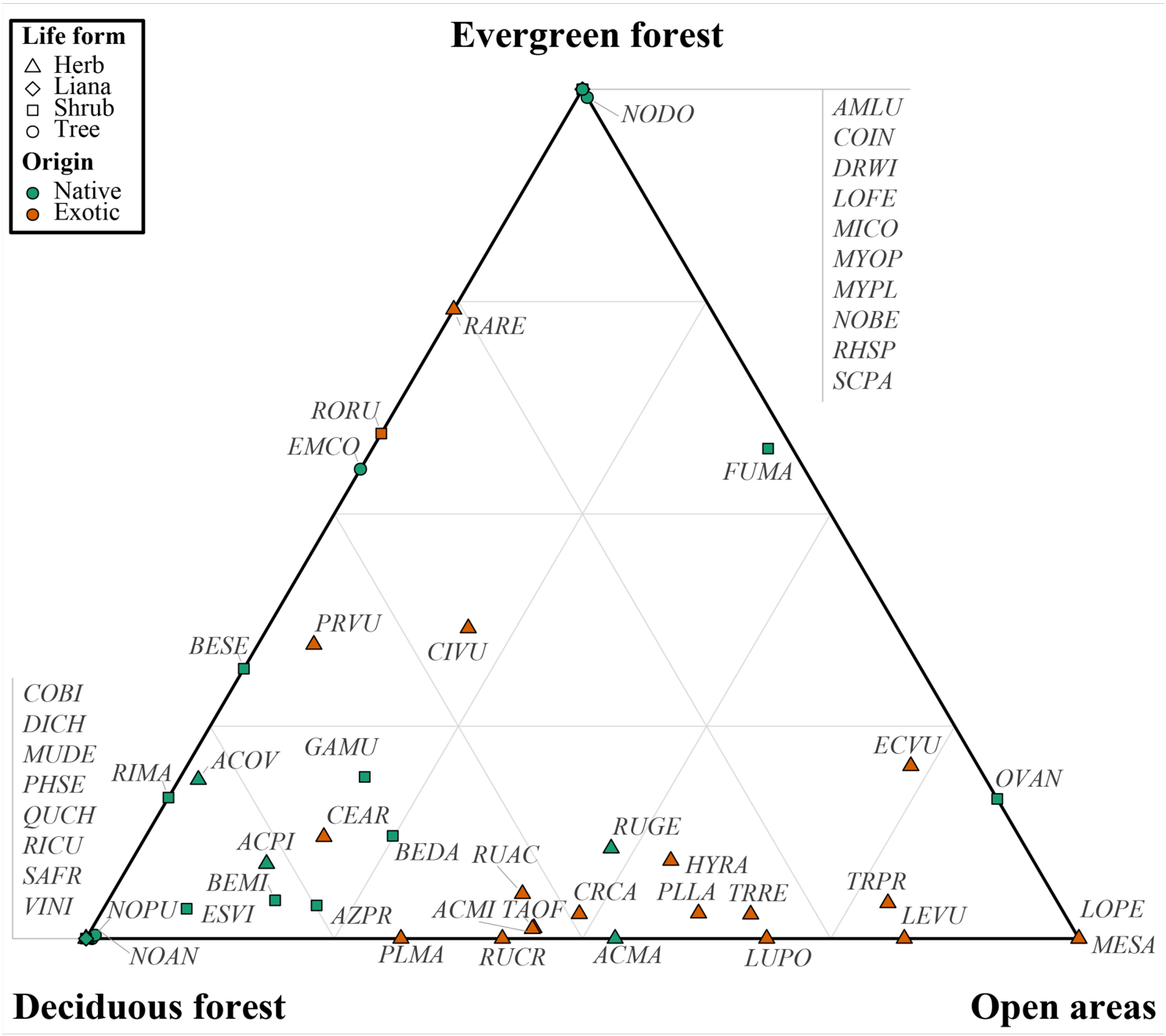


Figure 2

Configuration of the bee forage assemblage among land covers. Ternary diagram of the proportion of each species' biomass in deciduous forest, evergreen forest, and open areas. Species recorded in a single cover are stacked at the corresponding vertex and listed next to it. Species codes are given in Table A2.

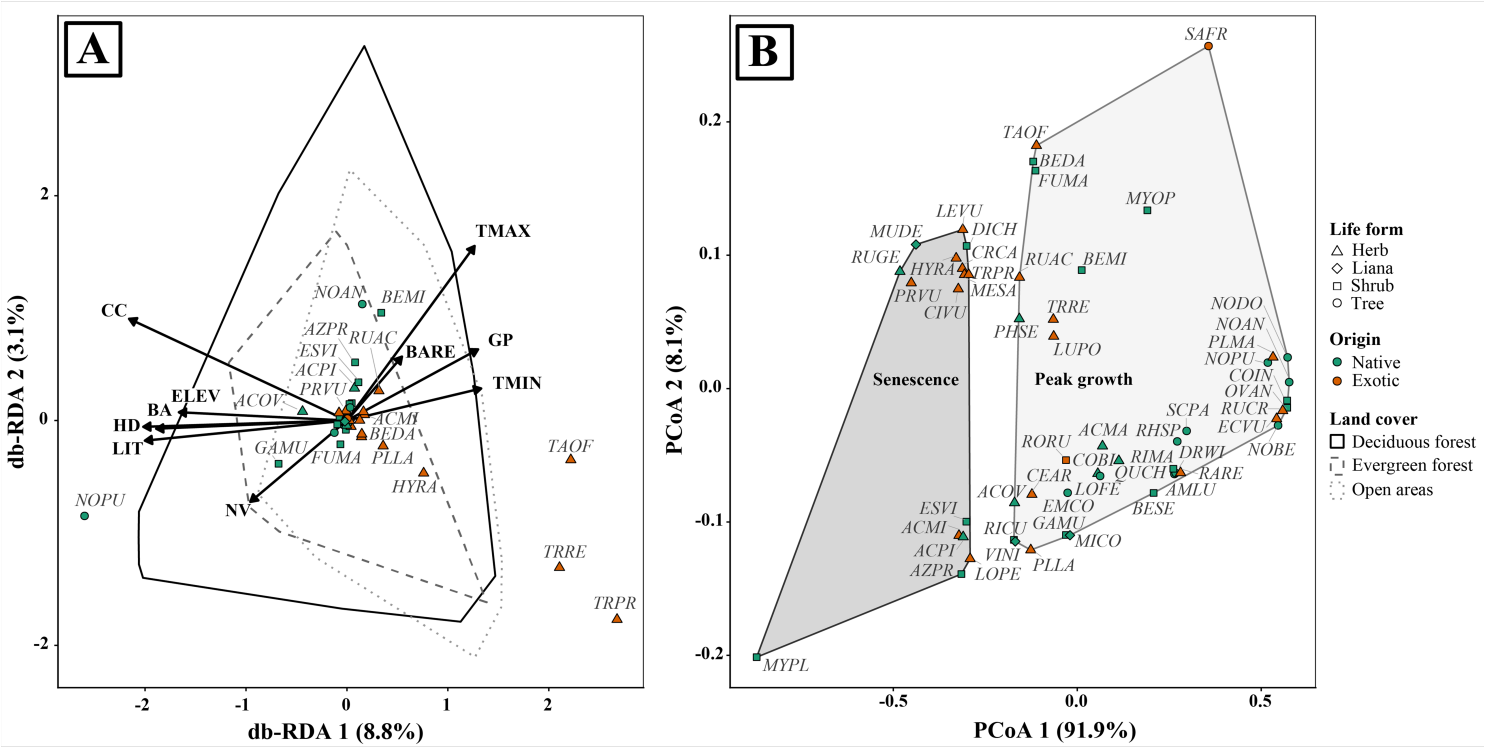


Figure 3

Ordination of bee forage supply in environmental space and in phenological trait space. (A) db-RDA of composition in relation to the ten drivers (arrows; CC, canopy cover; BA, basal area; HD, dominant height; LIT, litter; BARE, bare soil; NV, non-vascular cover; GP, grazing pressure; TMAX, maximum summer temperature; TMIN, minimum winter temperature; ELEV, elevation); outlines enclose the plots of each land cover, and the 18 species with the highest biomass are labelled. (B) PCoA of species according to their flowering profile; outlines group species by their main phenological phase, and points are jittered to separate species with identical flowering profiles. Species codes are given in Table A2.

Supplementary Files

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