

Invasion by *Ulex europaeus* L. and fire history: patterns in vegetation composition, diversity, and structure in Colombian páramos.

José Arnaldo Muñoz

jamunozd89@gmail.com

Universidad Nacional de Colombia - Sede Bogotá: Universidad Nacional de Colombia

<https://orcid.org/0000-0002-3291-3117>

Walter García-Suabita

Universidad Nacional de Colombia - Sede Bogotá: Universidad Nacional de Colombia

Dolors Armenteras-Pascual

Universidad Nacional de Colombia - Sede Bogotá: Universidad Nacional de Colombia

Research Article

Keywords: Invasive alien species, beta diversity, post-fire succession, indicator species, tropical high mountain ecosystems

Posted Date: September 8th, 2026

DOI: <https://doi.org/10.21203/rs.3.rs-10780919/v1>

License: © ⓘ This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

Invasion by *Ulex europaeus* L. and fire history: patterns in vegetation composition, diversity, and structure in Colombian páramos.

José A. Muñoz¹, jomunozd@unal.edu.co (correspondence)

Walter García-Suabita¹, walter.suabita@gmail.com

Dolores Armenteras Pascual^{1,2}, darmenterasp@unal.edu.co

¹Grupo de Investigación en Ecología del Paisaje y Modelación de Ecosistemas, Departamento de Biología, Facultad de Ciencias, Universidad Nacional de Colombia, Bogotá 111311, Colombia

²Consejo Superior de Investigaciones Científicas de España (CSIC), Madrid 28006, España

ORCID:

0000-0002-3291-3117 (JAM)

0000-0002-5559-8180 (WSG)

0000-0003-0922-7298 (DAP)

ABSTRACT

Tropical high-mountain ecosystems did not evolve under frequent fire regimes; however, the recent increase in fire occurrence and the expansion of invasive plants are transforming their plant communities. We evaluated vegetation composition, diversity, and structure across six locations in páramos and high Andean forest–páramo transition zones in the Colombian Eastern Cordillera, and their relation to invasion by *Ulex europaeus* L. and the time since the last recorded wildfire (TSLF). By establishing 25 × 2 m transects and 1-m² plots, we analyzed vegetation structure, estimated Hill numbers and beta diversity, assessed community composition via NMDS, PERMANOVA, and PERMDISP, and identified indicator species. We recorded 134 vascular plant species belonging to 90 genera and 50 families. Invaded sites presented lower evenness, greater dominance, and a simplified vertical structure. *U. europaeus* reached importance value index (IVI) values close to 34% and was the strongest indicator species of invaded sites (IndVal = 0.975), revealing a close association between invasion and community reorganization. Floristic composition differed among sites and along the TSLF gradient, although the latter pattern was associated with greater within-group heterogeneity. Beta diversity was dominated by species turnover. At Escobal, where it was already present before the fire, *U. europaeus* dominated the community after 3 years of recovery, a pattern consistent with potential invasion–fire feedback. These findings highlight the vulnerability of páramo ecosystems and the need for early detection and control of *U. europaeus*.

KEYWORDS

Invasive alien species, beta diversity, post-fire succession, indicator species, tropical high mountain ecosystems

INTRODUCTION

Andean páramo ecosystems occur in Colombia, Costa Rica, Ecuador, Peru, Panama, and Venezuela, extending above the continuous tree line and below the permanent snow line, generally between 2,800 and 4,700 m a.s.l. (Hofstede and Llambí 2020). Tropical high mountain ecosystems, particularly páramos, have not experienced frequent fires, although fires have occurred naturally since the Holocene and more frequently since human occupation (White 2013; Espinoza et al. 2022). The extent to which these ecosystems are adapted to wildfire remains under debate (Armenteras et al. 2020; Ocampo-Zuleta and Parrado-Rosselli 2023; Sabogal 2023). Although páramos can recover after fire, natural regeneration is slow (Vargas-Ríos et al. 2002; Zomer and Ramsay 2020), and their sensitivity means that increasing wildfire frequency and intensity may trigger irreversible degradation processes (Armenteras et al. 2021; Blake et al. 2023; Brück et al. 2023; Murad et al. 2024).

Approximately 15% of the total area of Andean páramos burned between 1985 and 2022 (Obando-Cabrera et al. 2025) has been driven by anthropogenic pressures and climatic factors (Armenteras et al. 2011; Borrelli et al. 2015; Díaz-Timoté et al. 2026). Together with other disturbances, wildfire facilitates the establishment and spread of invasive alien plants that can influence fire dynamics (Moscol-Olivera and Cleef 2009; Giraldo-Cañas 2010; Sandoya et al. 2017; Fusco et al. 2022; Giles et al. 2024).

Ulex europaeus L., commonly known in Colombia as “retamo espinoso”, is a shrub native to Europe that has been established across much of the Colombian Andes and reaches páramo areas up to 4,000 m a.s.l., with substantial ecological and economic impacts (Barrera-Cataño et al. 2019; Galappaththi et al. 2023; Díaz-Reyes et al. 2026). It is among the world’s most aggressive invasive species (Atlan et al. 2015; Roberts and Florentine 2021) and displays highly flammable traits associated with high-intensity wildfires (Anderson and Anderson 2010; Madrigal et al. 2012; Dent et al. 2019; Melnik et al. 2024). It displaces native flora, homogenizes community composition and structure, modifies fuels, and increases fire occurrence and spread (Marino et al. 2011; Madrigal et al. 2012; Altamirano et al. 2016; León-Cordero et al. 2016; Wyse et al. 2018). However, knowledge gaps regarding these processes persist in the Neotropics (Tomat-Kelly and Flory 2022).

In Colombia, *U. europaeus* is known to alter the communities it invades (Beltrán and Barrera-Cataño 2014; Ocampo-Zuleta and Solorza-Bejarano 2017; Ángel-Vallejo et al. 2025), influence wildfire dynamics, and benefit from fire (Barrera-Cataño et al. 2002; Fernández-Méndez et al. 2016; Ocampo-Zuleta and Beltrán-Vargas 2018). However, how these effects vary across post-fire regeneration scenarios in páramo and tropical high mountain ecosystems remains unknown. This gap is particularly relevant given the increasing occurrence of wildfires and because vegetation recovery occurs under simultaneous pressure from biological invasion, which may constrain the ecosystem’s successional trajectory (Barrera-Cataño et al. 2019; Tomat-Kelly and Flory 2022; Díaz-Reyes et al. 2026).

In this study, we evaluated changes in floristic composition, diversity, and vegetation structure in páramo communities and communities within the high Andean forest–páramo transition zone in relation to invasion status by *U. europaeus* and time since the last recorded wildfire (TSLF). Given its effects on native community composition and structure, and its association with fire, we expected that (i) invaded sites would exhibit lower evenness, greater dominance, and a more simplified vertical structure than non-invaded sites would; (ii) floristic composition would differ among sites and along the TSLF gradient; and (iii) nestedness would dominate over turnover in beta diversity at invaded sites, whereas the relative contribution of turnover would increase with TSLF at non-invaded sites.

MATERIALS AND METHODS

Study design

In this study, we employed an observational space-for-time substitution design, in which each combination of fire history, expressed as time since the last recorded wildfire (TSLF), and invasion status by *U. europaeus* was represented by a single geographic site. Each site was used as a representation of a contrasting stage of ecological succession in the vegetation communities of páramo ecosystems and the high Andean forest–páramo transition zone (Pickett 1989). Accordingly, each study site constituted a unique ecological unit in which site identity (i.e., location, elevation, land cover, disturbance regime, climate, soils, and other environmental conditions), TSLF, and invasion status covaried.

The study sites were selected on the basis of official vegetation-cover maps for the departments of Cundinamarca and Boyacá (IGAC 2021, 2022), previous knowledge of the study areas, and field surveys conducted to verify accessibility, presence of páramo vegetation or the high Andean forest–páramo transition zone, fire scars and the occurrence of *U. europaeus*. A site was considered invaded when established individuals of *U. europaeus* occurred as continuous cover or dense patches, accounting for more than 30% of the total area observed at the site. At non-invaded sites, no *U. europaeus* individuals were recorded in any vegetation strata or within an approximately 50-m radius of the sampling units.

The TSLF was assigned to each site on the basis of wildfire records from the environmental authority (CAR 2025), satellite-derived burned-area data published for the region (Obando-Cabrera et al. 2024), and local reports, considering a 25-year observation window (2000–2025). Sites for which no burned area was detected since 2000 via the available information were classified as “no recent fire,” without implying the absolute absence of historical fire.

Study area

The study was conducted on the western slope of the Colombian Eastern Cordillera, within the Cruz Verde–Sumapaz páramo complex (south of Bogotá and Soacha, Cundinamarca) and the Telecom and Merchán Páramos Protective Forest Reserve (Saboyá, Boyacá) (Fig. 1; Table 1). Three sampling sites were selected in Cruz Verde–Sumapaz. Batallon1 was located in the Usme district, near the boundary with the municipality of Une (4°22'50.55" N, 74°07'13.63" W), within the Instruction, Training, and Retraining Battalion (BITER 13) of the Colombian National Army. The vegetation at this site consisted of shrubland and grassland–frailejónal communities invaded by *U. europaeus*, with no record of recent fire. Batallon2 was located in the upper part of the slope, outside BITER 13 (4°22'45.92" N, 74°06'50.73" W, 3,238 m a.s.l.), within similar vegetation cover but without invasion and with approximately 25 years of post-fire recovery. Soacha was located in the San Jorge rural district, in the upper Soacha River basin, municipality of Soacha (4°29'24.54" N, 74°10'56.39" W, 3,260 m a.s.l.), within a high Andean forest–páramo transition zone, without *U. europaeus* invasion and with wildfire history in early 2013.

Three sites were also established in Telecom and Merchán. Telecom1 was located near the Alto Saboyá Military Base (5°42'46.65" N, 73°49'03.25" W, 3,240 m a.s.l.), in a fragmented páramo with shrubland and frailejónal–grassland vegetation invaded by *U. europaeus*. No fires had been recorded during the previous 25 years, although evidence of livestock grazing in earlier years was observed. Telecom2 was located in the same area (5°42'51.08" N, 73°49'07.55" W, 3,260 m a.s.l.) with similar vegetation cover but without invasion or records of recent fires. Given its history of disturbance associated with agricultural and livestock activities (CAR 2010), the Telecom páramo site was considered a contrasting instance for evaluating invasion under more prolonged post-fire recovery

periods (greater TSLF) relative to sites affected by recent fires. The final site, Escobal, was located in the upper part of the Escobal Alto rural district, near the boundary with the municipality of Albania, Santander (5°43'39.36" N, 73°47'43.90" W, 3,250 m a.s.l.). It was situated within a high Andean forest-páramo transition zone invaded by *U. europaeus* and affected by a wildfire in early 2023. Previous field surveys confirmed that *U. europaeus* was already established in the area before the fire event, which was corroborated by local residents.

In addition to differing in fire history and invasion status, the sites were contrasting in terms of climatic regime, soils, vegetation cover, slope, and other environmental conditions. These variables were therefore considered components of the ecological context of each scenario rather than factors independent of invasion status or TSLF.

Table 1. Description of the study sites. Source: IGAC (2001, 2004), IDEAM (2024).

Variable	Batallon1	Batallon2	Soacha	Telecom1	Telecom2	Escobal
Páramo	Cruz-Verde Sumapaz			Telecom and Merchán		
Mean elevation (m a.s.l.)	3185	3237	3254	3338	3344	3248
<i>Ulex</i> invasion status	Invaded	Non-invaded	Non-invaded	Invaded	Non-invaded	Invaded
Fire history (TSLF)	No recent fire	25 years	13 years	No recent fire		3 years
Climate classification (Caldas-Lang)	Humid lower páramo		Semiarid lower páramo	Humid lower páramo		
Mean annual precipitation	1500 – 2000 mm		500 -1000 mm	1500 – 2000 mm		
Mean annual temperature	9- 12 °C					
Topography	Moderately to steeply sloping relief (6% slope). Lower slope.	Moderately to steeply sloping relief (12.4% slope). Upper slope.	Steeply sloping (37.1% slope). Upper slope.	Moderately to strongly dissected and moderately escarped (10.3% slope).	Moderately to strongly escarped (9.1% slope).	Strongly escarped (23.5% slope). Upper slope.
Soils	Andisols and Inceptisols		Inceptisols	Inceptisols and Andisols		Entisols and Inceptisols

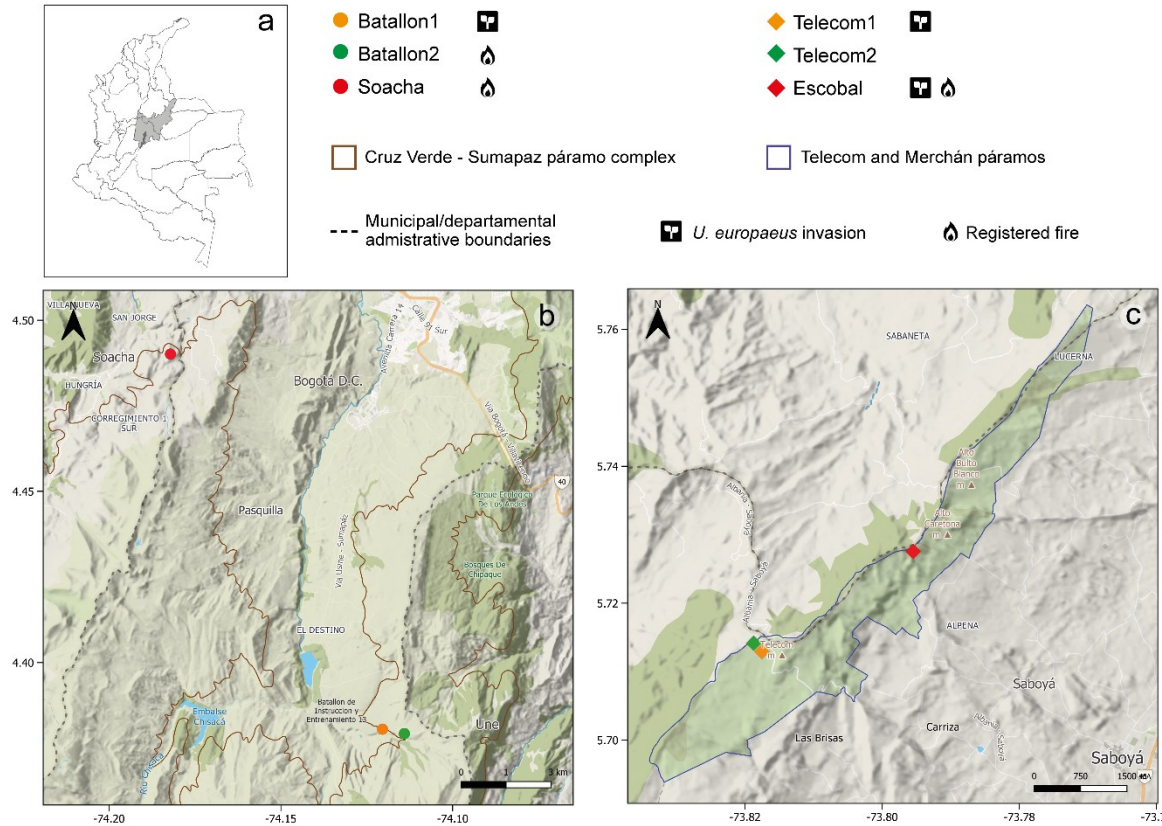


Fig. 1. Location map of the study sites (WGS84 datum). **a)** Cundinamarca and Boyacá departments (Colombia); **b)** sites in Cruz Verde–Sumapaz; **c)** sites in Telecom and Merchán.

Vegetation sampling

A total of 41 Gentry-type transects, each measuring 25×2 m (50 m^2), were established. This sampling design is appropriate for predominantly herbaceous and shrub-dominated vegetation with scattered tree elements (Mostacedo and Fredericksen 2000; Osinaga et al. 2014). Seven transects were established per site, except at Batallon1, where six transects were established because of safety restrictions during fieldwork. At Batallon1, Batallon2, Telecom1, and Telecom2, transects were located in areas invaded or uninvaded by *U. europaeus*, according to the conditions of each site; at Soacha and Escobal, transects were arranged along the slope. All transects were separated by at least 50 m.

Within each transect, we recorded all individuals whose stems had a basal diameter (BD) ≥ 2 cm and measured approximately 3 cm above ground level. For each individual, the diameter at breast height (DBH; measured at 1.3 m), when applicable, total height, and maximum and minimum crown diameters were also measured. For multistemmed shrubs, BD and DBH were measured for each stem, whereas crown diameters were recorded for each individual. Individuals of *Espeletia* spp. were included because of their dominance at several sites. For the prostrate and herbaceous strata, three 1-m^2 plots were placed at the beginning, middle, and end of each transect, yielding a total of 123 plots. The observed cover (%) of each species was recorded in these plots. Field work was conducted between March and September 2025. Taxonomic identification was conducted directly in the field, and verified via photographic records and herbarium specimens collected during sampling. Specimens were deposited in the Colombian National Herbarium (COL). When species-level identification was not possible, records were retained at the genus level.

We assessed spatial independence among transects using Global Moran's I, which is based on geographic coordinates and absolute slopes, with a spatial weight matrix derived from the two nearest neighbors within each site ($k = 2$). Additionally, for each pair of transects we calculated Pearson's correlation between geographic distance and Sørensen dissimilarity, which was based on species presence-absence data. The mean of the within-site estimated correlations was used as the global statistic. Significance in both analyses was assessed via 1000 site-restricted bootstrap iterations in R (R Core Team 2026), using the *sf* (Pebesma 2018) and *vegan* (Oksanen et al. 2022) packages.

Data analysis

For the vegetation structure analyses, we classified records into vertical strata according to Cabrera-Amaya (2021): prostrate stratum (0–10 cm in height), herbaceous stratum (10–50 cm), low shrub stratum (50 cm–1.5 m), high shrub stratum (1.5–3 m), lower subarborescent stratum (3–5 m), and upper subarborescent stratum (5–12 m). The records were also classified by growth form following Ramsay and Oxley (1997).

To integrate data from all sampling units, we estimated the crown cover (m^2) of individuals recorded in transects as the area of an ellipse ($A = \pi \times \frac{D1}{2} \times \frac{D2}{2}$) (Rangel and Velásquez 1997). In the plots, percentage cover was converted to m^2 ($A = \frac{\%C}{100} \times 1 m^2 \times n_{plots}$). For each site, the relative cover by vertical stratum or growth form was calculated as the proportion of its area relative to the total area recorded at that site, allowing proportional comparisons between sampling methods. In the plots, species cover did not exceed 100%, whereas in the transects, individual crowns were not restricted to the transect area when the crown projection extended beyond the sampling perimeter. This approach allows the proportional contribution of each vertical strata and growth form to the total recorded cover to be compared independently of the sampling method.

The horizontal and vertical vegetation structures were described via diameter classes (2-cm intervals) and height classes (0.5-m intervals), respectively. For multitemmed individuals, the equivalent basal diameter (BD_eq) was calculated as the square root of the sum of the basal areas of all stems (Magarik et al. 2020). Species dominance at each site was estimated via the (IVI). For the 1- m^2 plots, this index was calculated from the relative frequency and relative cover (adapted IVI) (Mostacedo and Fredericksen 2000).

To evaluate sampling effort and standardize comparisons among sites, we constructed rarefaction and interpolation/extrapolation curves from incidence–frequency matrices (Chao et al. 2014), with 1,000 bootstrap iterations, via the *iNEXT* package in R (Hsieh et al. 2016; R Core Team 2026). Each sampling unit was defined as a composite unit consisting of one 25 × 2 m transect and its three associated 1- m^2 plots. Within each site, the incidence frequency of a species was defined as the number of sampling units in which it occurred, either in the transect or in any of its three associated plots. Alpha diversity was estimated via Hill numbers: observed richness (qD_0), Shannon diversity (qD_1), and inverse Simpson diversity (qD_2) (Jost and González-Oreja 2012; Chao et al. 2021).

We examined differences in floristic composition associated with *U. europaeus* invasion status and TSLF nonmetric multidimensional scaling (NMDS) and permutational multivariate analysis of variance (PERMANOVA), complemented by tests for homogeneity of multivariate dispersions (PERMDISP). Analyses were conducted with 1,000 permutations on Bray–Curtis dissimilarity matrices, using abundance data for transects and frequency data for plots. The site category (invaded vs. non-invaded by *U. europaeus*) and TSLF (3, 13, and 25 years and no recent fire) were evaluated as independent factors via the *vegan* package in R (Oksanen et al. 2022). Additionally, indicator species for each spatial and temporal scenario were identified via indicator value indices (IndVal;

Dufrène and Legendre 1997) with the *indicspecies* package in R (De Cáceres and Legendre 2009); associations with $p \leq 0.05$ were considered significant.

The growth-form composition, used as a functional proxy, was compared between invaded and non-invaded sites via an exact PERMANOVA based on Sørensen dissimilarity and combined presence–absence data, complemented by PERMDISP and NMDS.

Finally, we assessed total beta diversity from species presence–absence matrices via Sørensen dissimilarity (β -SOR) and partitioned it into two components: species turnover (Simpson dissimilarity, β -SIM) and nestedness-resultant dissimilarity (β -SNE) (Baselga 2010; Souza et al. 2026). Analyses were conducted by site and TSLF category for both transects and plots. Because the number of sampling units differed among site-level analyses (Batallon1: $n = 6$; all other sites: $n = 7$) and TSLF categories (no recent fire: $n = 20$; 3, 13 and 25 years: $n = 7$ each), a common subsample size was set at $n = 5$ for site-level analyses and $n = 6$ for TSLF analyses, with random selection of subsets for each comparison. Calculations were performed via the *betapart* package, version 1.5.4 (Baselga and Orme 2012), in R (R Core Team 2026). Ninety-five percent confidence intervals were obtained via 1000 bootstrap iterations.

RESULTS

Floristic composition

We recorded a total of 134 vascular plant species, representing 90 genera and 50 botanical families (Table S1). Asteraceae was the most diverse family, with 25 species (18.7%) across nine genera. *Ageratina* and *Espeletia* were the most species-rich genera, with seven and five species, respectively. *U. europaeus* was the only Fabaceae species recorded.

Species richness and floristic composition varied among the six sites (Fig. S1). Batallon1 contained 29 species, 24 genera, and 15 families and, despite the dominance of *U. europaeus*, included shrubland- and frailejónal-associated species such as *Monticalia ledifolia*, *Linochilus rosmarinifolius*, *Vaccinium floribundum*, *Gaultheria anastomosans*, and *Espeletia grandiflora*. Batallon2 contained 40 species, 33 genera, and 22 families, including *Bucquetia glutinosa* and *Paepalanthus lindenii*. Soacha included 46 species, 41 genera, and 32 families, with a predominance of woody species characteristic of the high Andean forest–páramo transition zone, including *Miconia ligustrina*, *Morella parvifolia*, *Gaiadendron punctatum*, *Macleania rupestris*, and *Weinmannia tomentosa*.

In Boyacá, Telecom1 contained 55 species, 41 genera, and 24 families. *U. europaeus* was dominant at this site, together with *Espeletia argentea*, *G. anastomosans*, *Baccharis macrantha*, *M. parvifolia*, and *Espeletia saboyana*, a frailejón endemic to this páramo that was recently described (Becerra and Mavárez 2022). Telecom2 presented the highest richness, with 62 species, 47 genera, and 30 families; the most frequent species were *E. saboyana*, *E. argentea*, *M. ligustrina*, *M. parvifolia*, and *Parablechnum loxense*. Escobal contained 47 species, 41 genera, and 25 families. *Ulex europaeus* was the most prevalent species, whereas most other taxa occurred at low frequencies in transects and plots.

Sampling completeness and alpha diversity patterns

All sites achieved sample coverage of at least 85%, and extrapolations approached 100% coverage (Table S2). Uncertainty was moderate at the invaded sites (Batallon1, Batallon2, and Telecom1). Rarefaction and interpolation/extrapolation curves based on the sampling units revealed differences in the diversity patterns among the sites (Fig. 2a). Batallon1 exhibited the lowest evenness ($qD_1/qD_0 = 0.61$) and highest dominance ($1 - [qD_1/qD_0] = 0.39$). At this site, the qD_1 and qD_2 curves

progressively diverged from the observed richness (qD_0) as the sampling effort increased. A similar pattern was observed at Escobal and Telecom1.

Batallon2 showed moderate evenness (0.66) and relatively high dominance (0.34). In contrast, Telecom2 presented the highest diversity values, with the greatest observed richness, low dominance (0.27), and high evenness (0.73). Soacha had the highest evenness (0.79) and lowest dominance (0.21), and its qD_1 and qD_2 curves remained close to qD_0 .

When species diversity was evaluated as a function of sample coverage, sites in Saboyá showed higher diversity values than those in Sumapaz (Fig. 2b). At sites invaded by *U. europaeus* (Telecom1, Escobal, and Batallon1), the qD_1 and qD_2 curves diverged from the qD_0 curve as coverage increased, indicating lower evenness and a greater concentration of incidence frequencies in a few species. At non-invaded sites (Telecom2, Soacha, and Batallon2), curves for the three diversity orders remained close beyond 80% coverage, reflecting more homogeneous incidence distributions.

Vegetation structure

Among the total species identified, 42.5% were upright shrubs, 14.1% were herbs, 9.0% were trees, 9.0% were tussocks, 7.5% were basal rosettes, and 6.0% were prostrate herbs. The remaining 11.9% comprised less frequent growth forms, including prostrate shrubs, bambusoid species, stem rosettes, acaulescent rosettes, and climbing or trailing species (Table S1).

The vegetation structure varied considerably among the sites according to the disturbance scenario. After integrating the transects and plot records, the relative cover across all the sites in both Sumapaz and Saboyá was dominated by upright shrubs, whereas the high shrub and low shrub strata accounted for the largest proportion of the vertical structure (Fig. 3).

Sites invaded by *U. europaeus* presented a more simplified structure than the other sites did. The low shrub and high shrub layers accounted for the largest proportion of relative cover in areas dominated by upright shrubs, with limited representation of acaulescent rosettes and tussocks at Batallon1 and Escobal. At non-invaded sites (Batallon2, Telecom2, and Soacha), the distributions of cover among vertical strata were similar, but the growth forms were more diverse, including stem rosettes at Batallon2 and trees at Soacha and Telecom2.

Sites with a recent fire history presented contrasting patterns according to the TSLF. Batallon2 and Escobal presented greater relative representation of basal growth forms, including tussocks, acaulescent rosettes, and basal rosettes. At Soacha, trees represented the second most dominant growth form, whereas Telecom2 exhibited the greatest structural complexity among all sites, including an upper subarborescent strata.

In terms of horizontal structure, the diameter classes along the transects differed among the sites (Fig. 4). At Batallon1, Soacha, Telecom1, and Escobal, individuals were concentrated in the first three classes ($BD_{eq} < 8$ cm), resulting in a typical reverse J-shaped distribution, which was more pronounced at Soacha. This pattern is associated with dynamic communities characterized by active regeneration processes and continuous recruitment, with a high proportion of individuals in smaller classes and limited representation in larger classes. At Batallon2 and Telecom2, the distribution shifted toward intermediate classes, with peaks at 6–8 cm and 6–10 cm, respectively. At Batallon2, this shift was associated with the occurrence of *Espeletia grandiflora* individuals in the sample and with one of the longest TSLF values. At Telecom2, the distribution was irregular and extended into larger diameter classes ($BD_{eq} > 14$ cm), with the presence of *E. saboyana* individuals and other species with greater woody development.

The height distributions followed a similar pattern (Fig. 5). Except at Telecom2, most individuals were concentrated between 0.5 and 2.5 m in height, which is consistent with the predominance of upright shrubs and the herbaceous, low shrub, and high shrub layers. Telecom2 showed a broader distribution and a greater representation of individuals taller than 3 m, including *W. tomentosa* and species of *Miconia*.

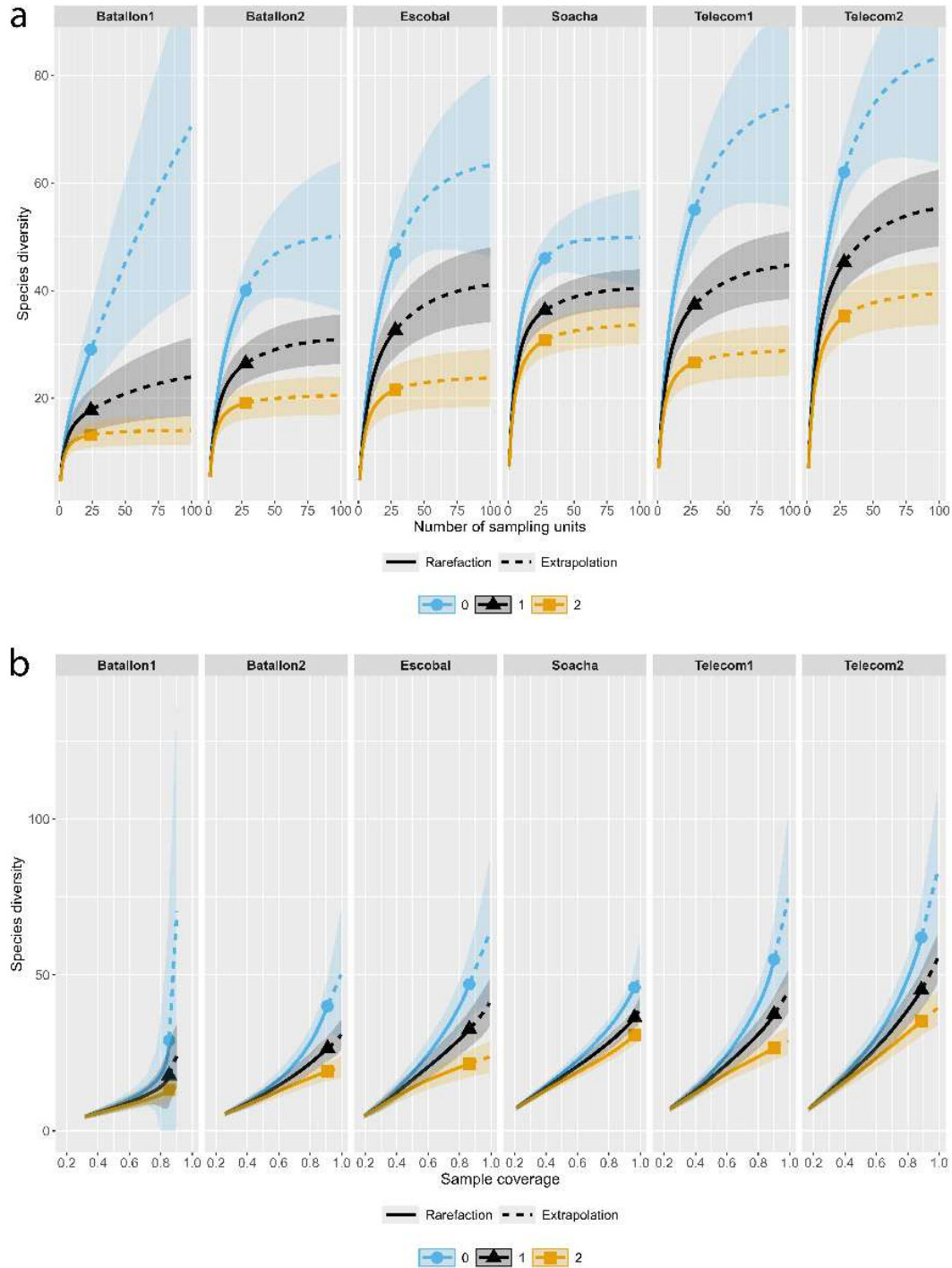


Fig. 2. Rarefaction and extrapolation curves based on incidence frequencies per sampling unit: (a) species diversity as a function of the number of sampling units; (b) species diversity as a function of sample coverage. The solid lines represent rarefaction curves, whereas the dashed lines represent extrapolation curves. The shaded areas indicate 95% confidence intervals. 0, order qD_0 ; 1: order qD_1 ; 2: order qD_2 .

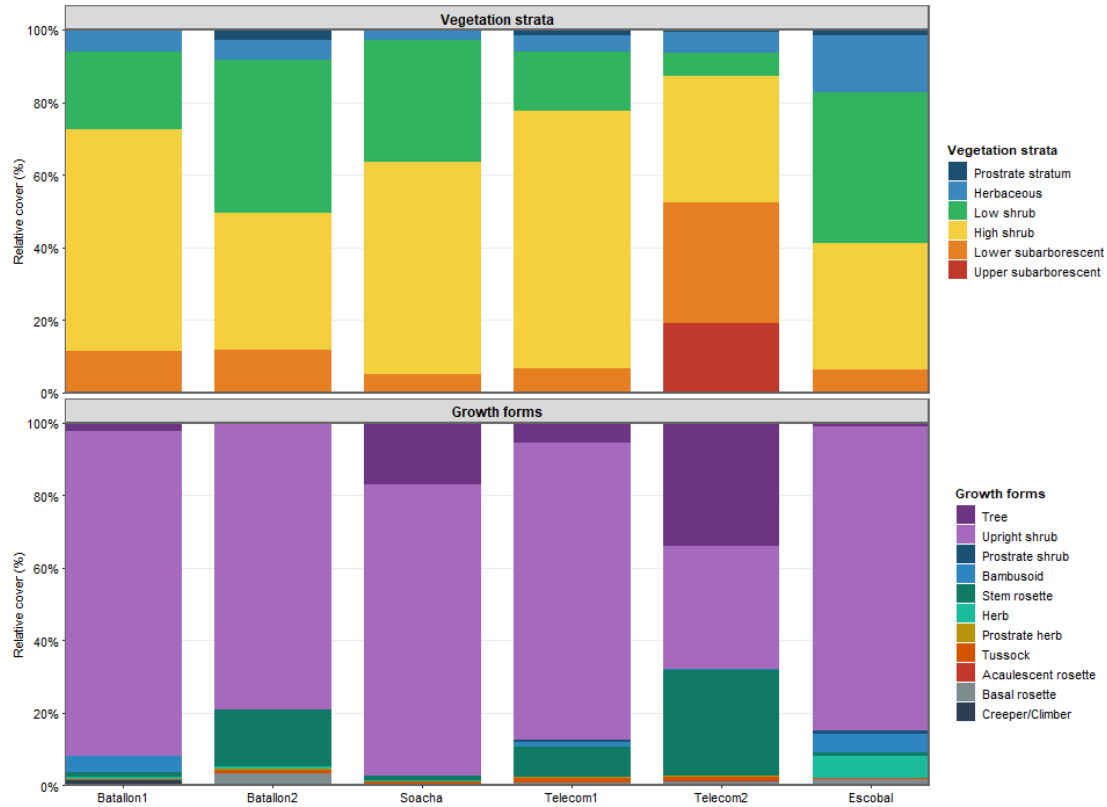


Fig. 3. Vegetation structure across the study sites. The relative contribution of each vertical stratum (top) and growth form (bottom) to the total cover recorded across the sampling units is shown.

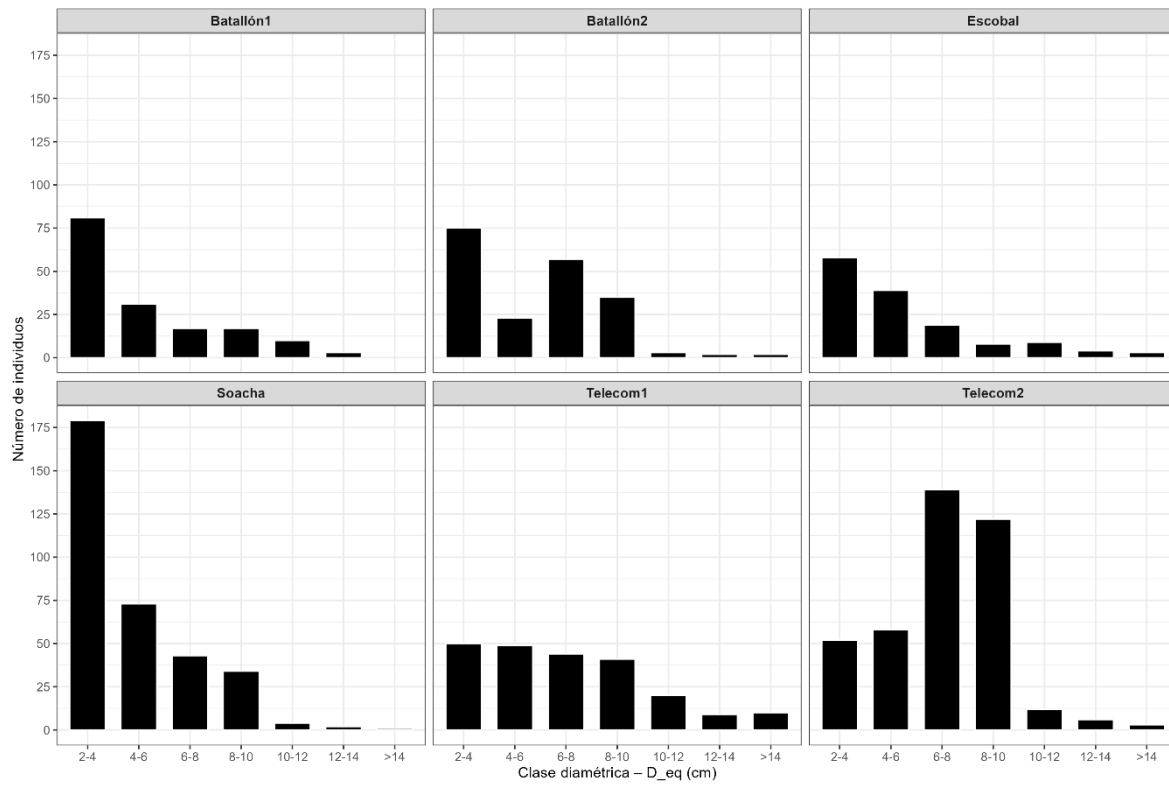


Fig. 4. Equivalent basal diameter classes (D_{eq}) in the vegetation transects across the study sites.

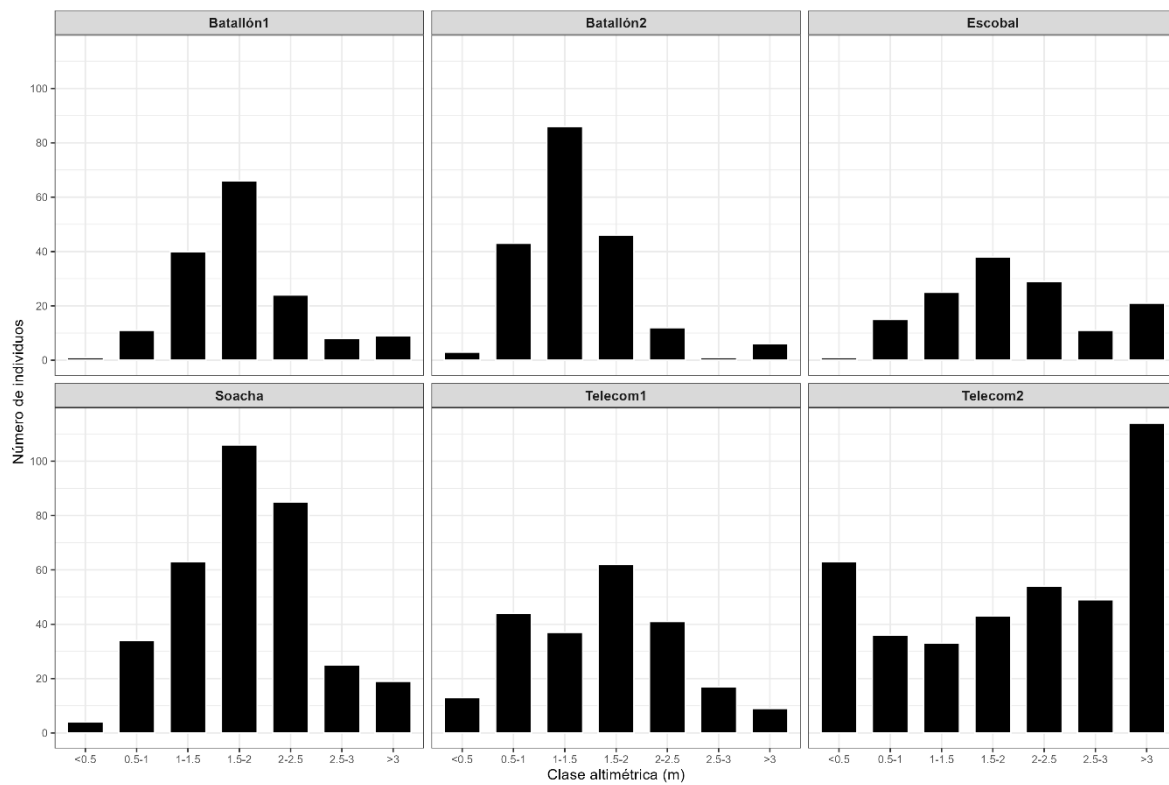


Fig. 5. Height classes in the vegetation transects across the study sites.

Species dominance

In the transect surveys, *U. europaeus* had the highest IVI at the invaded sites (Table S3). At Batallon1, it reached an IVI of 33.5%, followed by native species such as *M. ledifolia* (15.0%) and *A. tinifolia* (9.15%). At Telecom1, its IVI was greater (34.3%), whereas *E. argentea* (17.5%) and *M. parvifolia* (7.08%) were the native species with the highest IVI values. At Escobal, *U. europaeus* was also dominant, with an IVI of 26.0%, followed by *W. tomentosa* (13.2%) and *Cavendishia bracteata* (11.8%). Compared with Soacha, Escobal presented a greater contribution of tree elements and species typical of the high Andean forest–páramo transition zone.

At Batallon2, *E. grandiflora*, *M. ledifolia*, and *V. floribundum* presented the highest IVI values, at 30.1%, 13.8%, and 13.6%, respectively. At Soacha, *M. parvifolia* (18.8%) and *M. ligustrina* (16.8%) were codominant, and IVI was relatively evenly distributed among the remaining recorded species. In contrast, Telecom2 was dominated by *E. saboyana* (34.6%), *E. argentea* (12.8%), and *M. ligustrina* (8.7%), which are frequent species in this páramo.

In the plot surveys, *U. europaeus* remained the dominant taxon at Batallon1 (14.9%), Telecom1 (8.2%), and Escobal (11.9%) (Table S4). At Batallon2, *Paepalanthus lindenii* (11.8%) and *Gaultheria anastomosans* (10.9%) were dominant. At Soacha, IVI values did not exceed 7%, reflecting relatively even dominance among species; *G. hapalotricha* (6.9%) and *Arcytophyllum nitidum* (6.5%) presented the highest values. At Telecom2, *Parablechnum loxense* (8.1%) and *G. anastomosans* (6.5%) were the most representative species; *Lycopodium clavatum* and *E. argentea* were also among the ten species with the highest IVI values. Across all the sites, several Ericaceae species consistently occurred among the ten species with the highest IVI values.

Differences in floristic composition

Analyses were conducted separately for transects and plots. For transects, NMDS (stress = 0.156) showed moderate separation in floristic composition among sites (Fig. 6a). Escobal occupied a more extreme position in the ordination space, with dispersed values and an elongated ellipse, whereas Batallon1 formed a more compact group near the center of the NMDS ordination. Telecom2 occupied an intermediate position and showed some overlap with Batallon2, Soacha, and Telecom1, suggesting partially similar species compositions among these sites. PERMANOVA indicated a strong effect of site on the floristic composition of transects ($R^2 = 0.532$; $F = 7.972$; $p = 0.001$), whereas PERMDISP revealed that differences in dispersion among sites were not significant ($F = 2.138$; $p = 0.082$). These findings suggest that the PERMANOVA results primarily reflected differences in floristic composition among transects rather than within-group heterogeneity among communities.

When transects were grouped by TSLF, NMDS revealed differentiated ellipses, although with some overlap in the central region of the ordination space (Fig. 6b). PERMANOVA indicated significant differences in transect composition among temporal groups ($R^2 = 0.342$; $F = 6.405$; $p = 0.001$). However, PERMDISP also indicated significant differences in dispersion among TSLF categories ($F = 10.675$; $p = 0.001$), suggesting that, in addition to floristic differentiation, there was substantial within-group heterogeneity among communities in each temporal group. This pattern was particularly evident in the no-recent-fire category, which included three sites with contrasting invasion statuses (Batallon1 and Telecom1, invaded; Telecom2, non-invaded).

For the plots, NMDS (stress = 0.188) revealed moderate overlap among the site ellipses and greater within-site dispersion than transects (Fig. 7a). Escobal and Batallon2 showed differentiated compositions, whereas Telecom1, Telecom2, and Batallon1 overlapped extensively. Soacha formed a more compact group and was positioned toward more extreme values along NMDS1 relative to the other sites. PERMANOVA indicated a significant effect of site on species composition ($R^2 = 0.411$;

$F = 4.891$; $p = 0.001$), whereas PERMDISP detected no significant differences in dispersion among sites ($F = 1.502$; $p = 0.227$). These results suggest that site effects primarily reflect compositional differences rather than variations in within-group heterogeneity among communities at this sampling scale.

When the plots were grouped according to the TSLF (Fig. 7b), the temporal groups presented differentiated ellipses with overlap in the central region of the ordination space. Compared with the other temporal groups, Escobal (TSLF = 3 years) presented the greatest within-group dispersion and a distinct position. In contrast, sites without records of recent fires and Soacha overlapped, indicating greater similarity in community composition. PERMANOVA detected significant differences in species composition among temporal groups ($R^2 = 0.296$; $F = 5.198$; $p = 0.001$). Nevertheless, PERMDISP also indicated significant differences in dispersion among groups ($F = 4.256$; $p = 0.010$), indicating that the effect of TSLF on species composition in plots was associated not only with differences in typical community composition but also with variation in within-group heterogeneity among communities within each temporal category.

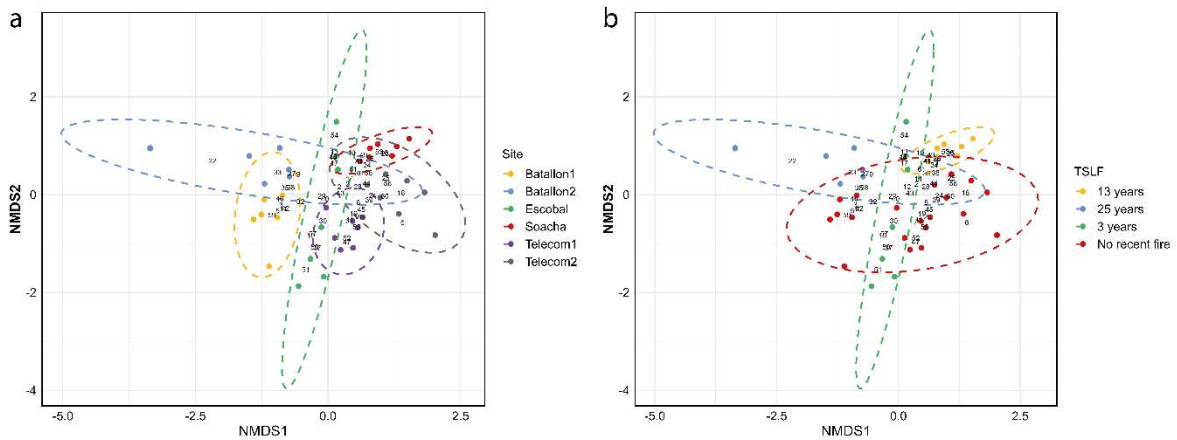


Fig. 6. NMDS ordination of the floristic composition of the vegetation communities in the 25×2 m transects: a) ordination by site, and b) ordination by the TSLF.

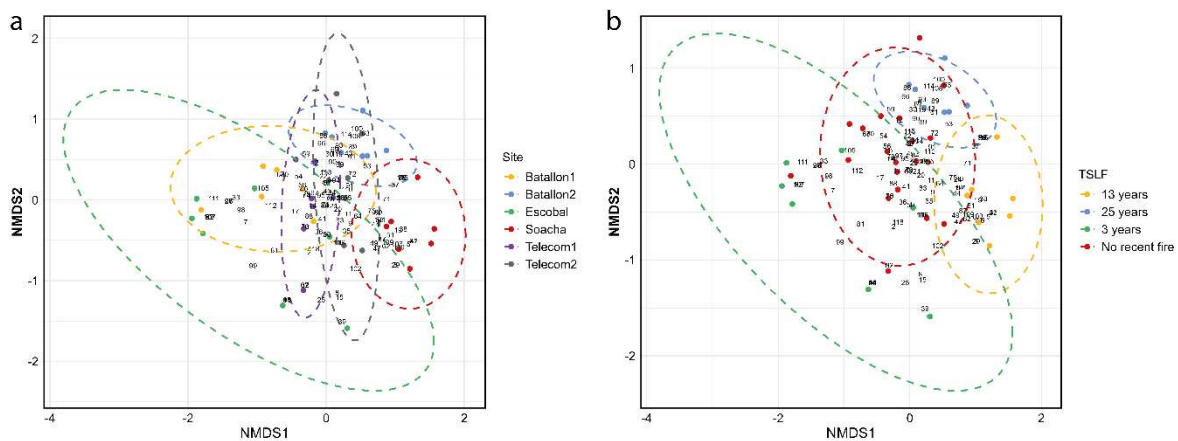


Fig. 7. NMDS ordination of floristic composition in vegetation communities sampled in 1 m^2 plots: a) ordination by site, and b) ordination by TSLF.

Functional filtering

No significant differences were detected in growth form composition between invaded and non-invaded sites (PERMANOVA, $R^2 = 0.035$; $F = 2.888$; $p = 0.500$) or in multivariate dispersion between the two groups (PERMDISP, $F = 1.664$; $p = 0.191$). Similarly, NMDS (stress = 0.14) showed broad dispersion and considerable overlap between invasion statuses (Fig. 8). Because the exact PERMANOVA was performed using six sites grouped into two conditions (three invaded vs. three non-invaded), only 10 possible partitions could be evaluated; therefore, the minimum attainable p value was 0.1.

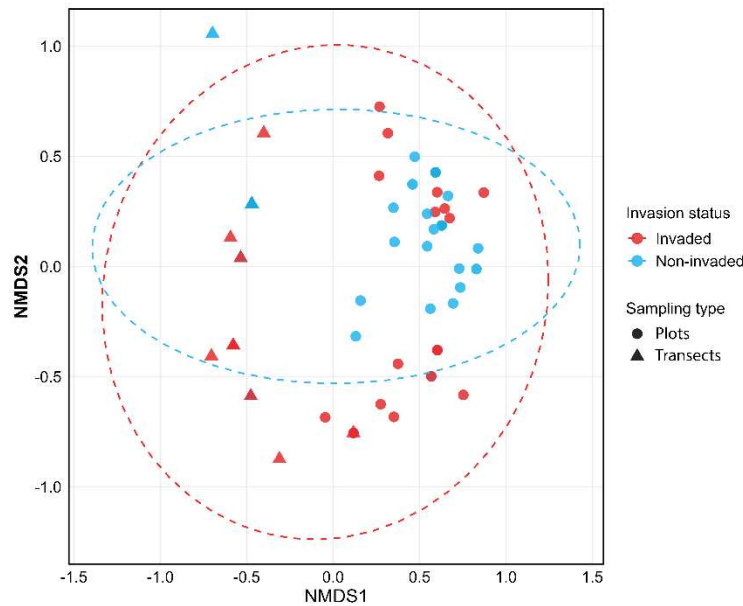


Fig. 8. NMDS ordination of growth-form composition between invaded and non-invaded sites and by sampling method.

Beta diversity analysis

Site-level beta diversity, considering the presence or absence of *U. europaeus*, was high. Escobal and Telecom2 presented the highest observed β -SOR values, at 0.811 and 0.722, respectively, with distributions concentrated in high-dissimilarity ranges and broad, in some cases multimodal, curves (Fig. 9a; Table 2). Although Batallon1 (β -SOR = 0.615) and Soacha (β -SOR = 0.611) had the lowest observed β -SOR values, their distributions extended toward intermediate dissimilarity ranges. All distributions showed partial overlap. Turnover was the predominant component of β -SOR, with β -SIM values ranging from 0.400 at Batallon2 to 0.735 at Escobal. Escobal presented a combination of high β -SOR and β -SIM values, whereas Batallon1, Soacha, Telecom1, and Telecom2 presented moderate turnover ($0.429 \leq \beta$ -SIM ≤ 0.615). In contrast, nestedness made a smaller contribution to beta diversity, with observed β -SNE values ranging from 0.079 at Telecom1 to 0.273 at Batallon2.

In the TSLF analysis, β -SOR was high across all temporal groups, with observed values ranging from 0.614 (TSLF = 13 years) to 0.850 (no recent fire). The distributions of the 3-year, 13-year, and no-recent-fire groups partially overlapped (Fig. 9b; Table 3). The same pattern observed at the site level was detected across TSLF categories: β -SIM dominated over β -SNE in all groups. The observed β -SIMs ranged from 0.500 (TSLF = 13 and 25 years) to 0.816 (no recent fire). The observed β -SNE values ranged from 0.034 (no recent fire) to 0.212 (TSLF = 25 years). In the latter group, the observed nestedness was greater than that in the other groups, and its distributions shifted toward high-

dissimilarity values, suggesting a relatively greater contribution of β -SNE to β -SOR within this temporal category.

For the 1 m² plots, β -SOR was also high across all the sites, with observed values ranging from 0.675 at Soacha to 0.821 at Escobal. Telecom1 and Telecom2 presented intermediate values (β -SOR = 0.697 and 0.733, respectively) (Fig. 10a; Table 4). The bootstrap distributions by site partially overlapped but were concentrated in high-dissimilarity ranges. In the transects, β -SIM were the dominant component of beta diversity, ranging from 0.579 at Batallon1 to 0.767 at Escobal. Escobal showed the same pattern observed in the transects, with high β -SOR and β -SIM values, suggesting substantial species turnover among the plots. Soacha, Telecom1, and Telecom2 exhibited moderate turnover ($0.623 \leq \beta$ -SIM ≤ 0.664), whereas Batallon1 and Batallon2 presented lower turnover (β -SIM = 0.579 and 0.632, respectively). Similarly, β -SNE made a smaller contribution to beta diversity at most sites, with observed values ranging from 0.034 at Telecom1 to 0.167 at Batallon1.

When analyzed according to TSLF, beta diversity was also high across all temporal groups, with observed β -SOR values ranging from 0.705 (TSLF = 13 years) to 0.829 (TSLF = 3 years) (Fig. 10b; Table 5). The distributions partially overlapped, but the 3-year and no-recent-fire groups were concentrated in higher dissimilarity ranges than the other groups were. Similarly, species turnover dominated over nestedness across all TSLF categories, with observed β -SIM values ranging from 0.575 (TSLF = 25 years) to 0.766 (TSLF = 3 years). The observed β -SNE values ranged from 0.047 (TSLF = 13 years) to 0.140 (TSLF = 25 years), with the latter group showing distributions that shifted toward higher nestedness values than the other groups did.

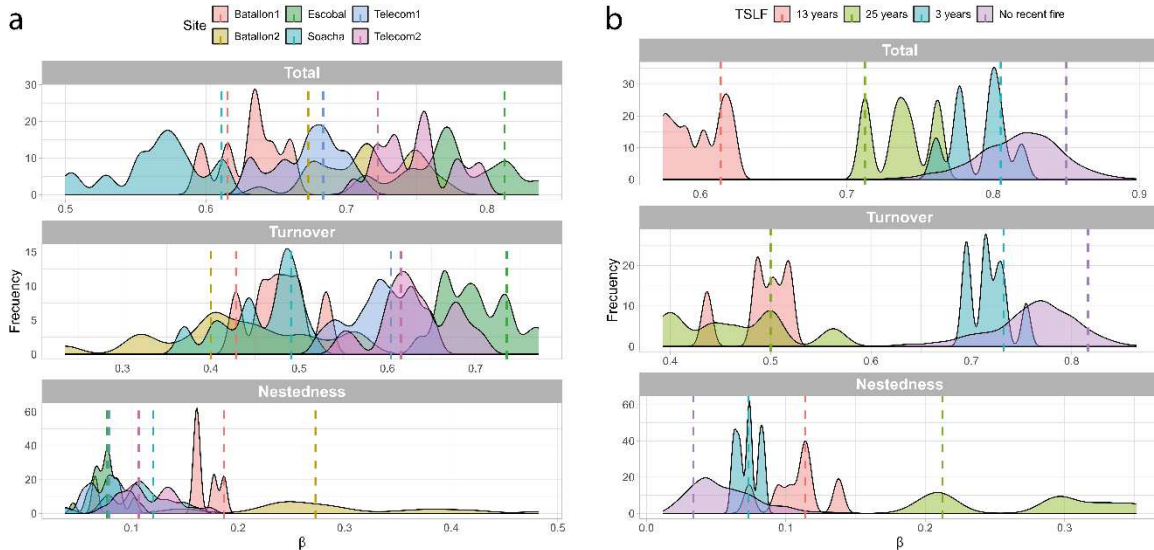


Fig. 9. Components of beta diversity in the study communities on the basis of data recorded in 25 × 2 m transects. The density plots show the distribution of values obtained through bootstrap resampling, and the dashed lines indicate the observed values of each component: a) by study site and b) by TSLF.

Table 2. Beta diversity (β -Sor), species turnover (β -Sim) and nestedness (β -Sne) of plant communities sampled from 25 × 2 m transects by study site. The 95% CIs were estimated via bootstrap resampling.

Site	β -SOR-Obs	β -SOR-media	β -SOR-IC	β -SIM-Obs	β -SIM-media	β -SIM-IC	β -SNE-Obs	β -SNE-Media	β -SNE-IC
Batallon1	0.615	0.631	0.596 – 0.660	0.429	0.479	0.429 – 0.531	0.187	0.152	0.066 – 0.187
Batallon2	0.673	0.716	0.638 – 0.771	0.400	0.430	0.235 – 0.567	0.273	0.286	0.138 – 0.482

Escobal	0.813	0.775	0.712 – 0.837	0.735	0.700	0.636 – 0.771	0.077	0.075	0.045 – 0.104
Soacha	0.611	0.566	0.500 – 0.614	0.491	0.458	0.370 – 0.516	0.120	0.108	0.041 – 0.163
Telecom1	0.683	0.673	0.630 – 0.712	0.604	0.596	0.523 – 0.652	0.079	0.077	0.038 – 0.109
Telecom2	0.722	0.750	0.705 – 0.797	0.615	0.634	0.548 – 0.707	0.107	0.117	0.073 – 0.173

Table 3. Beta diversity (β -Sor), species turnover (β -Sim) and nestedness (β -SNe) of plant communities sampled in 25×2 m transects by TSLF. The 95% CIs were estimated via bootstrap resampling.

TSLF	β -SOR-Obs	β -SOR-media	β -SOR-IC	β -SIM-Obs	β -SIM-media	β -SIM-IC	β -SNE-Obs	β -SNE-Media	β -SNE-IC
3 years	0.805	0.791	0.761 – 0.819	0.732	0.718	0.694 – 0.755	0.073	0.073	0.062 – 0.084
13 years	0.614	0.599	0.574 – 0.622	0.500	0.491	0.437 – 0.519	0.114	0.108	0.074 – 0.138
25 years	0.712	0.738	0.712 – 0.763	0.500	0.465	0.393 – 0.563	0.212	0.273	0.200 – 0.352
No recent fire	0.850	0.818	0.756 – 0.870	0.816	0.762	0.667 – 0.836	0.034	0.056	0.020 – 0.112

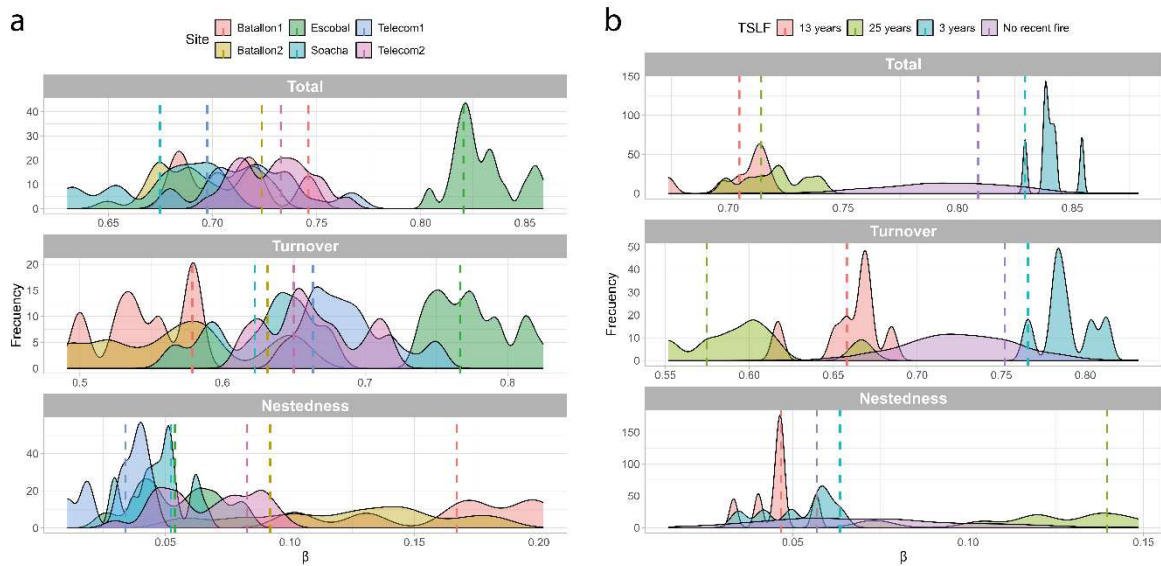


Fig. 10. Components of beta diversity in the study communities on the basis of data recorded in 1 m^2 plots. The density plots show the distribution of values obtained through bootstrap resampling, and the dashed lines indicate the observed values of each component: a) by study site and b) by TSLF.

Table 4. Beta diversity (β -Sor), species turnover (β -Sim) and nestedness (β -SNe) of plant communities sampled in 1 m^2 plots by study site. The 95% CIs were estimated via bootstrap resampling.

Site	β -SOR-Obs	β -SOR-media	β -SOR-IC	β -SIM-Obs	β -SIM-media	β -SIM-IC	β -SNE-Obs	β -SNE-Media	β -SNE-IC
Batallon1	0.746	0.709	0.682 – 0.746	0.579	0.546	0.500 – 0.580	0.167	0.162	0.102 – 0.202
Batallon2	0.724	0.696	0.649 – 0.730	0.632	0.572	0.491 – 0.657	0.092	0.123	0.057 – 0.183
Escobal	0.821	0.830	0.804 – 0.859	0.767	0.775	0.738 – 0.825	0.054	0.055	0.024 – 0.082
Soacha	0.675	0.677	0.630 – 0.709	0.623	0.629	0.564 – 0.676	0.052	0.047	0.028 – 0.067

Telecom1	0.697	0.720	0.678 – 0.769	0.664	0.688	0.642 – 0.752	0.034	0.032	0.011 – 0.046
Telecom2	0.733	0.730	0.698 – 0.765	0.650	0.662	0.613 – 0.717	0.083	0.067	0.030 – 0.097

Table 5. Beta diversity (β -Sor), species turnover (β -Sim) and nestedness (β -SNe) of plant communities sampled in 1 m² plots by TSLF. The 95% CIs were estimated via bootstrap resampling.

TSLF	β -SOR- Obs	β -SOR- media	β -SOR- IC	β -SIM- Obs	β -SIM- media	β -SIM- IC	β -SNE- Obs	β -SNE- Media	β -SNE - IC
3 years	0.829	0.841	0.829 – 0.854	0.766	0.789	0.766 – 0.813	0.063	0.052	0.035 – 0.063
13 years	0.705	0.705	0.674 – 0.718	0.658	0.660	0.617- 0.685	0.047	0.045	0.033 – 0.057
25 years	0.714	0.720	0.699 – 0.740	0.575	0.600	0.552 – 0.667	0.140	0.120	0.073 – 0.147
No recent fire	0.809	0.796	0.742 – 0.845	0.752	0.725	0.656 – 0.789	0.057	0.071	0.025 – 0.124

When the TSLF was examined within non-invaded sites, transect β -SOR increased along the temporal gradient from Soacha (TSLF = 13 years, β -SOR = 0.629) to Telecom2 (no recent fire, β -SOR = 0.789). The distributions partially overlapped but showed a progressive shift toward higher dissimilarity ranges at Batallon2 and Telecom2 (Fig. 11a; Table 6). Species turnover clearly dominated over nestedness at all three sites, with β -SIM values ranging from 0.524 at Soacha to 0.684 at Telecom2 (Batallon2: β -SIM = 0.500). The β -SIM distributions suggested greater species replacement among transects toward the no-recent-fire end of the temporal gradient. In contrast, nestedness showed similar observed values at Soacha and Telecom2 (β -SNE = 0.105) and a higher value at Batallon2 (β -SNE = 0.258); at the latter site, distributions were shifted toward higher nestedness values than at the other two sites.

In the plots, total beta diversity also increased slightly along the temporal gradient: Soacha (TSLF = 13 years, β -SOR = 0.728), Batallon2 (TSLF = 25 years, β -SOR = 0.740), and Telecom2 (no recent fire, β -SOR = 0.771). The β -SOR distributions overlapped, but the no-recent-fire group was concentrated in relatively high dissimilarity ranges, which was consistent with greater compositional differentiation among the plots (Fig. 11b; Table 7). Turnover was also the dominant component, with observed β -SIM values ranging from 0.625 at Batallon2 to 0.711 at Telecom2 (Soacha: β -SIM = 0.685). In contrast, β -SNE was relatively low at Soacha (β -SNE = 0.043) and Telecom2 (β -SNE = 0.059), with higher values at Batallon2 (β -SNE = 0.115).

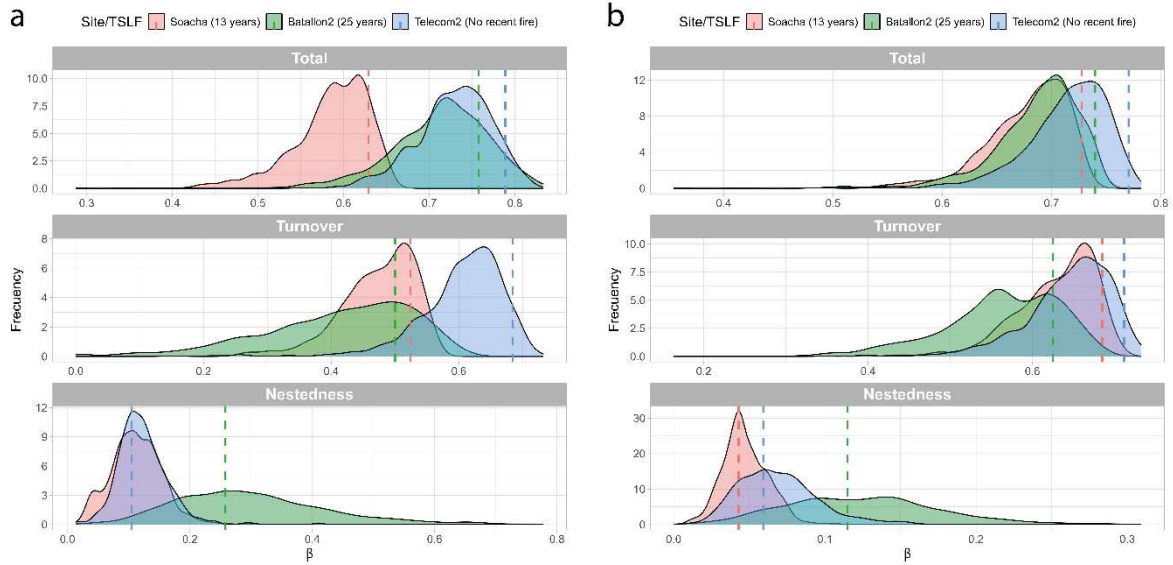


Fig. 11. Components of beta diversity in non-invaded study communities based on data recorded in a) 25×2 m transects and b) 1 m^2 plots, according to the TSLF. The density plots show the distribution of values obtained through bootstrap resampling, and the dashed lines indicate the observed values of each component.

Table 6. Beta diversity ($\beta\text{-Sor}$), species turnover ($\beta\text{-Sim}$) and nestedness ($\beta\text{-Sne}$) of non-invaded plant communities sampled from 25×2 m transects. The 95% CIs were estimated via bootstrap resampling.

Site	$\beta\text{-SOR-Obs}$	$\beta\text{-SOR-media}$	$\beta\text{-SOR-IC}$	$\beta\text{-SIM-Obs}$	$\beta\text{-SIM-media}$	$\beta\text{-SIM-IC}$	$\beta\text{-SNE-Obs}$	$\beta\text{-SNE-Media}$	$\beta\text{-SNE-IC}$
Soacha (13 y)	0.629	0.585	0.607 – 0.658	0.524	0.473	0.469 – 0.568	0.105	0.112	0.034 – 0.186
Batallon2 (25 y)	0.758	0.713	0.706 – 0.833	0.500	0.411	0.320 – 0.603	0.258	0.302	0.055 – 0.494
Telecom2 (No recent fire)	0.789	0.729	0.776 – 0.822	0.684	0.606	0.663 – 0.732	0.105	0.123	0.018 – 0.167

Table 7. Beta diversity ($\beta\text{-Sor}$), species turnover ($\beta\text{-Sim}$) and nestedness ($\beta\text{-Sne}$) of non-invaded plant communities sampled from 1 m^2 plots. The 95% CIs were estimated via bootstrap resampling.

Site	$\beta\text{-SOR-Obs}$	$\beta\text{-SOR-media}$	$\beta\text{-SOR-IC}$	$\beta\text{-SIM-Obs}$	$\beta\text{-SIM-media}$	$\beta\text{-SIM-IC}$	$\beta\text{-SNE-Obs}$	$\beta\text{-SNE-Media}$	$\beta\text{-SNE-IC}$
Soacha (13 y)	0.728	0.677	0.728 – 0.738	0.685	0.629	0.675 – 0.710	0.043	0.047	0.014 – 0.072
Batallon2 (25 y)	0.740	0.687	0.739 – 0.750	0.625	0.562	0.547 – 0.689	0.115	0.125	0.033 – 0.223
Telecom2 (No recent fire)	0.771	0.715	0.772 – 0.782	0.711	0.645	0.702 – 0.732	0.059	0.070	0.022 – 0.111

Indicator species

Among the transects, *U. europaeus* had the highest indicator value among the species associated with invaded sites ($\text{IndVal} = 0.975$, $p = 0.001$), those associated with sites without recent fires and those associated with a TSLF = 3 years ($\text{IndVal} = 0.839$, $p = 0.001$). At Batallon2, *E. grandiflora* was the indicator species associated with both the site ($\text{IndVal} = 0.864$, $p = 0.001$) and the TSLF = 25-year group ($\text{IndVal} = 0.906$, $p = 0.001$). Soacha had the greatest number of indicator species per treatment (≥ 5 species), including *M. parvifolia* ($\text{IndVal} = 0.944$, $p = 0.001$) (Table S5).

In the plots, *Brachyotum strigosum* and *Rhynchospora macrochaeta* were associated with Soacha both by site and by TSLF (IndVal = 1 and 0.926, respectively; $p = 0.001$). At Batallon2, *Paepalanthus lindenii* was the indicator species (IndVal = 1, $p = 0.001$). Soacha also had the greatest number of indicator species both by site (9 species) and by TSLF (10 species) (Table S6).

DISCUSSION

Structural simplification associated with invasion

Invasion by *U. europaeus* was associated with strong dominance and reduced evenness in the study communities. At the invaded sites, it reached the highest importance value index (IVI) values (33.5% at Batallon1 and 34.3% at Telecom1 on the transects), and the communities presented low evenness and high dominance according to the Hill numbers (e.g., $qD_1/qD_0 = 0.61$ at Batallon1). The separation among the qD_0 , qD_1 , and qD_2 curves at invaded sites is consistent with the invasion dynamics reported for this fabaceous shrub, indicating that reduced observed richness was accompanied by a disproportionate distribution of incidence frequencies (Broadfield and McHenry 2019; Roberts and Florentine 2021). This pattern is consistent with the biotic homogenization described for communities invaded by dominant competitive species (Daru et al. 2021; Lázaro-Lobo et al. 2023) and with the structural effects reported for *U. europaeus* in forest–grassland mosaics in southern Brazil (León-Cordero et al. 2016).

The simplification of the vertical structure at invaded sites, characterized by the concentration of relative cover in the herbaceous, low shrub, and high shrub layers, together with the predominance of upright shrubs and limited representation of acaulescent rosettes, tussocks, and stem rosettes, suggests that *U. europaeus* not only reduces species diversity but also reorganizes community architecture. In Brazil, *U. europaeus* has been reported to displace native herbaceous and shrub species, leading to more homogeneous communities with lower strata diversity (León-Cordero et al. 2016). This effect may be facilitated by the formation of a dense spiny canopy, the accumulation of standing necromass, and nitrogen fixation, which may favor this species relative to the local flora (Roberts and Florentine 2021; Kato-Noguchi and Kato 2025).

In Saboyá, Telecom1 (invaded) and Telecom2 (non-invaded) represent the least confounded contrast within the study design for examining the association with *U. europaeus* invasion. Both sites have comparable elevations and climatic regimes, similar disturbance histories, and represent the longest TSLF category (no recent fires). Telecom2 was the reference site with the highest apparent vegetation integrity, the greatest observed richness (62 species), the lowest dominance (0.27), and the highest evenness (0.73) among all the study sites; *E. saboyana*, a frailejón endemic to this páramo and recently described species (Becerra and Mavárez 2022), was dominant. This site also presented the most developed vertical structure, with 52.5% of relative cover occurring in the lower and upper subarborescent strata. This contrast indicates that, in the absence of additional pressure from recent fires, *U. europaeus* invasion was associated with reduced effective richness and evenness, resulting in marked changes in community organization (Roberts and Florentine 2021; Wang et al. 2025; Díaz-Reyes et al. 2026).

These patterns of structural simplification and dominance are consistent with the possibility that *U. europaeus* may act as an ecological filter on native vegetation, favoring some functional traits over others, as has been documented for other invasive species (Castro-Díez et al. 2016; Sodhi et al. 2019). However, when growth forms were used as a categorical proxy for functional traits and compared between invaded and non-invaded sites, no significant differences were detected in either functional composition (PERMANOVA, $R^2 = 0.035$; $F = 2.888$; $p = 0.500$) or dispersion (PERMDISP, $F = 1.664$; $p = 0.191$). This absence of a detectable signal is consistent with the scale of the analysis (three

invaded and three non-invaded sites), which imposed a structural constraint on the statistical test, with a minimum attainable p-value of 0.1 irrespective of the magnitude of the observed effect. Moreover, growth form cannot capture finer-scale traits, such as resprouting capacity, rooting depth, or leaf area, which could differ substantially between communities invaded by *U. europaeus* and those without invasion (Gallien and Carboni 2016; Fried et al. 2019). Consequently, based on the evidence presented here, it cannot be confirmed whether *U. europaeus* exerts an ecological filtering effect in the studied páramo ecosystems and high Andean forest–páramo transition zones.

Differences in floristic composition and diversity

Floristic composition varied consistently among sites and along the TSLF gradient in both transects and plots (PERMANOVA, $p = 0.001$ in all cases). However, the dispersion pattern assessed by PERMDISP reflects this ecological signal. The site variable explained 53.2% of the variation in composition in transects and 41.1% in plots, and the non-significant PERMDISP results ($F = 2.138$, $p = 0.082$ for transects; $F = 1.502$, $p = 0.227$ for plots) indicated turnover in floristic identity among the group centroids. In contrast, although the TSLF explained 34.2% of the variation in transects and 29.6% in plots, the significant PERMDISP results indicated that this effect also involved substantial within-group heterogeneity. This pattern is consistent with the no-recent-fire category, which includes sites with contrasting invasion statuses and disturbance histories (Batallon1 and Telecom1, invaded; Telecom2, non-invaded). The combination of centroid divergence and dispersion heterogeneity associated with time since disturbance has been reported in post-fire chronosequences in other landscapes, where ignoring within-group dispersion may lead to overinterpretation of PERMANOVA differences as evidence of the expected successional trajectory (Torres et al. 2022).

Species turnover (β -SIM) dominated over nestedness (β -SNE) in total beta diversity (β -SOR) across all the scenarios, both by site and TSLF, and in both transects and plots. Whereas β -SNE values were low in all cases ($0.032 \leq \beta\text{-SNE} \leq 0.273$), β -SIM accounted for the largest proportion of dissimilarity (e.g., $\beta\text{-SIM} = 0.816$ in the no-recent-fire group for transects). We predicted that nestedness would be the dominant component, assuming that fire and invasion would impoverish the shared regional floristic pool, as has been reported for other invasive species (Stotz et al. 2019). Contrary to this expectation, the observed pattern suggests that the study communities retain distinct floristic pools and is consistent with the possibility that different post-fire successional stages are associated with different species assemblages (Zomer and Ramsay 2021).

Similarly, in the analysis of TSLF within non-invaded sites, Telecom2 (no recent fire) presented the highest species turnover ($\beta\text{-SIM} = 0.684$ in transects and $\beta\text{-SIM} = 0.711$ in plots). Considering the history of agricultural and livestock disturbances in this area, this finding may indicate floristic differentiation associated with more advanced post-fire successional stages in the absence of additional pressure from *U. europaeus*. Although the pattern was not progressive, the results are consistent with a greater contribution of turnover to beta diversity in these scenarios, tending to increase toward the no-recent-fire end of the TSLF gradient. Fitzpatrick et al. (2013) and Li et al. (2024) reported similar patterns in long-term chronosequences, in which species turnover among communities increased as succession progressed, reflecting greater differentiation among assemblages over time.

Jiang et al. (2023) described similar patterns in woody communities exposed to multiple environmental gradients, in which greater environmental heterogeneity increased the relative contribution of turnover to total beta diversity. However, because the study sites combined contrasting climatic regimes, soils, elevations, post-fire recovery periods, and invasion statuses, the contribution of each factor to species turnover cannot be isolated independently. Similarly, in burned Mediterranean shrublands, turnover was greater even between early and late successional stages,

highlighting the roles of dispersal and high floristic heterogeneity among patches at different stages (Torres et al. 2022). In regenerating subtropical forests, turnover has also been associated with deterministic community assembly during succession (Guclu et al. 2024).

The bootstrap distributions of these components were generally broad and partially overlapped among sites and TSLF groups, and several showed multimodal curves in analyses based on the minimum subsample size. This pattern is consistent with the high ecological heterogeneity among sites and unequal sample sizes (Batallon1, $n = 6$; all other sites, $n = 7$). In species abundance distributions, modality has been reported to increase with ecological variability and the spatial extent of communities (Antão et al. 2017).

Indicator species and Ericaceae persistence

Different Ericaceae species were recurrent among taxa with high IVI values across all the sites, regardless of invasion status or TSLF. Taxa such as *V. floribundum*, *G. anastomosans*, and *M. rupestris* cooccur with *U. europaeus* at invaded sites, in contrast with the limited representation of non-woody growth forms in these areas. This pattern suggests that functional attributes of Ericaceae, such as clonal regeneration and resprouting from belowground or basal structures, may enable them to persist under invasion and fire (Clarke et al. 2013; Gil-Romera et al. 2019), as reported by Ocampo-Zuleta and Parrado-Rosselli (2023) during early post-fire stages in subpáramo vegetation in the Bogotá Eastern Hills (Cruz Verde–Sumapaz complex). Thus, Ericaceae persistence may be associated with functional resistance to invasion, although it does not seem to counteract the loss of evenness or structural simplification induced by *U. europaeus*.

This floristic asymmetry was also evident in the indicator species analysis. The occurrence of several exclusive taxa with high IndVal values at Soacha and Batallon2 is consistent with non-invaded communities retaining greater floristic heterogeneity and being better suited to reflecting transitions in ecological succession (Jakovac et al. 2022), suggesting a more active successional trajectory than at invaded sites.

Non-invaded sites therefore provide a reference for potential successional trajectories. Soacha, located in the high Andean forest–páramo transition zone, which has a drier climate and has experienced more than a decade without wildfire, exhibited high evenness ($qD_1/qD_0 = 0.79$) and cover dominated by the high shrub and low shrub strata, with a substantial contribution of trees. Telecom2, in turn, presented the most complex vertical structure, with high cover in the lower and upper subarborescent strata. Batallon2, with 25 years of recovery, presented a shift in diameter distribution toward intermediate classes and high turnover. *E. grandiflora* was an indicator species in this sector, both by site (IndVal = 0.864) and TSLF (IndVal = 0.906), and has been reported to tolerate environmental stress and fire and to codominate during advanced successional stages (Sarmiento et al. 2003; Zomer and Ramsay 2018). These sites indicate the successional direction that Escobal might follow in the absence of pressure from *U. europaeus*, supporting the use of the TSLF as a reference for interpreting ecological recovery while acknowledging the limitations of the study design.

Invasion–fire cycle in páramo ecosystems

The Escobal site illustrates the coupling between invasion and fire. *U. europaeus* was present before the 2023 wildfire and, after only 3 years of recovery, was already dominant (IVI = 26.0% in transects and 11.9% in plots). It was also the strongest indicator species of invaded sites (IndVal = 0.975, $p = 0.001$) and of the no-recent-fire and shortest-TSLF (3-year) scenarios (IndVal = 0.839, $p = 0.001$). Because *U. europaeus* combines high flammability with rapid post-fire colonization through mass germination from its heat-stimulated soil seed bank (Anderson and Anderson 2010; Madrigal et al. 2012; Dent et al. 2019; Roberts and Florentine 2021), its early establishment may initiate positive feedback; the invasion–fire cycle described in other ecosystems (Fusco et al. 2022; Tomat-Kelly and

Flory 2023). In the absence of fire, full dominance generally occurs 7–15 years after initial establishment (Beltrán and Barrera-Cataño 2014; León-Cordero et al. 2016). Therefore, Escobal's trajectory suggests that, without intervention, post-fire regeneration in the presence of *U. europaeus* may shift toward an invasive species-dominated state.

Design limitations and management implications

The patterns described here should be interpreted considering the limitations inherent to the observational space-for-time substitution design (Pickett 1989). Because each combination of TSLF and invasion status was represented by a single site, site identity—including elevation, soils, slope, climatic regime, and disturbance history—covaried with the variables of interest. Therefore, the variation explained by “site” in the PERMANOVA cannot be attributed exclusively to invasion or fire. Although the absence of spatial and floristic autocorrelation among transects within each site was confirmed, this assessment operated at a different scale and did not eliminate confounding factors at the site level.

The TSLF was reconstructed from records spanning the last 25 years; therefore, “no recent fire” indicates the absence of records within that temporal window but not necessarily the historical absence of fire. This uncertainty increases when disturbance history is considered, a limitation consistent with criticisms of space-for-time substitution approaches when the number of sites per treatment combination is low (Damgaard 2019). Studies including more sites per condition and, where possible, a crossed invasion × TSLF design would allow these effects to be disentangled. Nevertheless, the observed patterns are consistent with the literature on the effects of *U. europaeus* and fire on plant communities and provide a relevant contribution to the Neotropics, where knowledge gaps persist regarding interactions between invasive species and fire in tropical high mountain ecosystems (Tomat-Kelly and Flory 2023).

The association between pre-fire invasion and early post-fire dominance at Escobal provides sufficient warning to prioritize the prevention and early control of *U. europaeus* in páramo and high Andean forest ecosystems with a fire history. Restoration experiences in páramos degraded by exotic forest plantations (Escobar et al. 2021) show that reversing structural changes in high mountain vegetation is a slow and uncertain process, reinforcing the value of preventive action. Detecting and removing juvenile and adult individuals, with the aim of depleting the soil seed bank before dominance becomes established (Ocampo-Zuleta and Solorza-Bejarano 2017; Barrera-Cataño et al. 2019), would likely be more effective than ecological restoration once invasion–fire feedback has been established.

CONCLUSIONS

This study revealed that invasion by *U. europaeus* was strongly associated with lower evenness, greater dominance, and a simplified vertical structure, a pattern consistent with this species' capacity to reorganize the architecture of the communities it invades. Floristic composition varied significantly among sites and across TSLF categories; however, much of the variation associated with TSLF reflected differences in dispersion among groups rather than an ordered turnover of dominant species because the recent-fire category included sites with contrasting invasion statuses and disturbance histories. Although the observational design did not allow confirmation of the ecological mechanisms underlying these associations, the results provide a sufficient warning to support early management of this species in páramos with a recent fire history.

Beta diversity was dominated by species turnover rather than nestedness at both invaded and non-invaded sites, contrary to expectations under the assumption that the simultaneous occurrence of fire and invasion would impoverish the shared floristic pool. This finding indicates that differences among

communities result from the replacement of distinct species assemblages rather than from the progressive impoverishment of a common regional floristic pool, although bootstrap distributions indicate high within-group heterogeneity that should be interpreted with its associated uncertainty. The recurrence of Ericaceae among the species with the highest importance values suggests the existence of a subset of native flora with functionally resistant traits in the face of *U. europaeus* and fire, possibly associated with resprouting from basal and belowground structures. The patterns at Soacha and Batallon2 indicate that, in the absence of invasion, post-fire communities may follow successional trajectories toward more complex structures.

The case of Escobal—a site with recent fires and pre-fire invasion, where *U. europaeus* rapidly became dominant after a fire—is consistent with the potential occurrence of an invasion–fire cycle in the high Andean forest–páramo transition zone, although the study design did not allow this mechanism to be demonstrated conclusively. This pattern suggests that sites affected by both fire and *U. europaeus* invasion may be at risk of shifting toward species-poor successional states that are difficult to reverse. Therefore, the most efficient management strategy should focus on preventing new invasion foci and periodically removing seedlings and juvenile individuals to deplete the soil seed bank before high dominance is attained, in conjunction with long-term ecological restoration and adaptive management.

Future studies using crossed designs (invaded/non-invaded $\times$ TSLF gradients), spatial replication, demographic monitoring, and functional-trait measurements will help quantify the synergistic effects of invasion and fire and advance spatial modeling of invasion–fire cycle risk under climate-change scenarios.

Data availability

The data supporting the findings of this study are available from the corresponding author upon reasonable request.

Acknowledgments

We thank Juan Camilo Murcia, Arnold García, Sergio Arévalo, Carlos Solano, and Jimmy Soler for their assistance with fieldwork; Carlos Suárez and Diego Cabrera-Amaya for their support with species identification; Andrés Del Risco for English-language editing and grammatical review of the final version of the manuscript; and the Universidad Nacional de Colombia for providing access to laboratory facilities and workspace.

Author Contributions

Conceptualization: JAM and DAP. Fieldwork and laboratory work: JAM. Data curation: JAM and WGS. Statistical analysis: WGS and JAM. Writing the original draft: JAM. Writing, review and editing: JAM and DAP. All the authors have read and agreed to the submitted version of the manuscript.

Funding

JAM received support from the Bicentennial Doctoral Excellence Scholarship, Cohort II, funded by the Science, Technology and Innovation Fund of Colombia's General Royalties System (Department of Cundinamarca) (BPIN 2021000100003).

Declarations**Competing Interests**

The authors have no relevant financial or nonfinancial interests to disclose.

References

- Altamirano A, Cely JP, Etter A, et al (2016) The invasive species *Ulex europaeus* (Fabaceae) shows high dynamism in a fragmented landscape of south-central Chile. *Environ Monit Assess* 188:495. <https://doi.org/10.1007/s10661-016-5498-6>
- Anderson SAJ, Anderson WR (2010) Ignition and fire spread thresholds in gorse (*Ulex europaeus*). *Int J Wildland Fire* 19:589–598. <https://doi.org/10.1071/WF09008>
- Ángel-Vallejo MC, García-Marín EJ, Feuillet-Hurtado C, et al (2025) Spatial variability in early reproductive characteristics of *Ulex europaeus* L. (Fabaceae) invading in the high-mountain of central Colombia. *Acta Oecologica* 128:104098. <https://doi.org/10.1016/j.actao.2025.104098>
- Antão LH, Connolly SR, Magurran AE, et al (2017) Prevalence of multimodal species abundance distributions is linked to spatial and taxonomic breadth. *Global Ecology and Biogeography* 26:203–215. <https://doi.org/10.1111/geb.12532>
- Armenteras D, Dávalos LM, Barreto JS, et al (2021) Fire-induced loss of the world's most biodiverse forests in Latin America. *Science Advances* 7:eabd3357. <https://doi.org/10.1126/sciadv.abd3357>
- Armenteras D, González TM, Vargas Ríos O, et al (2020) Incendios en ecosistemas del norte de Suramérica: avances en la ecología del fuego tropical en Colombia, Ecuador y Perú. *Caldasia* 42:1–16. <https://doi.org/10.15446/caldasia.v42n1.77353>
- Armenteras D, Retana-Alumbreros J, Molowny-Horas R, et al (2011) Characterizing fire spatial pattern interactions with climate and vegetation in Colombia. *Agricultural and Forest Meteorology* 151:279–289. <https://doi.org/10.1016/j.agrformet.2010.11.002>
- Atlan A, Schermann -Legionnet Agnès, Udo N, Tarayre M (2015) Self-Incompatibility in *Ulex europaeus*: Variations in Native and Invaded Regions. *International Journal of Plant Sciences* 176:515–524. <https://doi.org/10.1086/681669>
- Barrera Cataño JI, Rojas Rojas JE, Contreras-Rodríguez SM (eds) (2019) Plan de prevención, manejo y control de las especies de retamo espinoso (*Ulex europaeus*) y retamo liso (*Genista monspessulana*) en la jurisdicción CAR, Primera edición. Pontificia Universidad Javeriana, Bogotá
- Barrera-Cataño JI, Ríos-Alzate HF, Pinzón-Osorio CA (2002) Planteamiento de la propuesta de restauración ecológica de áreas afectadas por el fuego y/o invadidas por el retamo espinoso (*Ulex europaeus* L.) en los cerros de Bogotá D.C. *Pérez-Arbelaesia* 55–71
- Baselga A (2010) Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography* 19:134–143. <https://doi.org/10.1111/j.1466-8238.2009.00490.x>
- Baselga A, Orme CDL (2012) betapart: an R package for the study of beta diversity. *Methods in Ecology and Evolution* 3:808–812. <https://doi.org/10.1111/j.2041-210X.2012.00224.x>
- Becerra MT, Mavárez J (2022) *Espeletia saboyana* (Milleriaceae, Asteraceae), a New Critically Endangered Caulirosula from Cordillera Oriental, Colombia. *Systematic Botany* 47:593–606. <https://doi.org/10.1600/036364422X16516711856571>
- Beltrán HE, Barrera-Cataño JI (2014) Caracterización de invasiones de *Ulex europaeus* L. de diferentes edades como herramienta para la restauración ecológica de bosques altoandinos, Colombia. *Biota Colombiana* 15:

Blake LJ, Chohan JK, Escobar MP (2023) Agro-extractivism and neoliberal conservation: *campesino* abandonment in the Boyacá páramos, Colombia. *Journal of Rural Studies* 102:103071. <https://doi.org/10.1016/j.jrurstud.2023.103071>

Borrelli P, Armenteras D, Panagos P, et al (2015) The Implications of Fire Management in the Andean Paramo: A Preliminary Assessment Using Satellite Remote Sensing. *Remote Sensing* 7:11061–11082. <https://doi.org/10.3390/rs70911061>

Broadfield N, McHenry MT (2019) A World of Gorse: Persistence of *Ulex europaeus* in Managed Landscapes. *Plants* 8:523. <https://doi.org/10.3390/plants8110523>

Brück SA, Torres BDM, de Moraes Polizeli M de LT (2023) The Ecuadorian paramo in danger: What we know and what might be learned from northern wetlands. *Global Ecology and Conservation* 47:e02639. <https://doi.org/10.1016/j.gecco.2023.e02639>

Cabrera-Amaya DM (2021) Riqueza, composición florística y estructura de la vegetación silvestre en la zona rural de las cuencas de las quebradas Yomasa y Fucha, Bogotá, Colombia. *Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales* 45:761–776. <https://doi.org/10.18257/raccefyn.1255>

Corporación Autónoma Regional de Cundinamarca (CAR) (2010) Plan de manejo ambiental: Reserva Forestal Protectora Páramos de Telecom y Merchán. <https://runapadmin.parquesnacionales.gov.co/default/general/descargarplan?pid=101>

Corporación Autónoma Regional de Cundinamarca (CAR) (2025) Registro de Eventos. Portal de Datos Geográficos CAR. https://datosgeograficos.car.gov.co/datasets/deb311dfbc5f4949a7b82fd57f0fd488_19/explore?location=5.727359,-73.781946,15.

Castro-Díez P, Pauchard A, Traveset A, Vilà M (2016) Linking the impacts of plant invasion on community functional structure and ecosystem properties. *Journal of Vegetation Science* 27:1233–1242. <https://doi.org/10.1111/jvs.12429>

Chao A, Gotelli NJ, Hsieh TC, et al (2014) Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecological Monographs* 84:45–67. <https://doi.org/10.1890/13-0133.1>

Chao A, Henderson PA, Chiu C-H, et al (2021) Measuring temporal change in alpha diversity: A framework integrating taxonomic, phylogenetic and functional diversity and the iNEXT.3D standardization. *Methods in Ecology and Evolution* 12:1926–1940. <https://doi.org/10.1111/2041-210X.13682>

Clarke PJ, Lawes MJ, Midgley JJ, et al (2013) Resprouting as a key functional trait: how buds, protection and resources drive persistence after fire. *New Phytologist* 197:19–35. <https://doi.org/10.1111/nph.12001>

Damgaard C (2019) A Critique of the Space-for-Time Substitution Practice in Community Ecology. *Trends in Ecology & Evolution* 34:416–421. <https://doi.org/10.1016/j.tree.2019.01.013>

Daru BH, Davies TJ, Willis CG, et al (2021) Widespread homogenization of plant communities in the Anthropocene. *Nat Commun* 12:6983. <https://doi.org/10.1038/s41467-021-27186-8>

De Cáceres M, Legendre P (2009) Associations between species and groups of sites: indices and statistical inference. *Ecology* 90:3566–3574. <https://doi.org/10.1890/08-1823.1>

Dent JM, Buckley HL, Lustig A, Curran TJ (2019) Flame Temperatures Saturate with Increasing Dead Material in *Ulex europaeus*, but Flame Duration, Fuel Consumption and Overall Flammability Continue to Increase. *Fire* 2:6. <https://doi.org/10.3390/fire2010006>

Díaz-Reyes A, Aguirre-Acosta N, Feuillet-Hurtado C, Rodríguez-Rey GT (2026) Population genomics of *Ulex europaeus* in the Northern Andes: insights into an invasive species in high-mountain ecosystems. *Plant Ecology and Evolution* 159:106–122. <https://doi.org/10.5091/plecevo.165188>

Díaz-Timoté JJ, Obando-Cabrera L, Alvarado ST, Hantson S (2026) Drivers and Spatial Patterns of Burned Area in High-Andean Páramos. *Fire* 9:95. <https://doi.org/10.3390/fire9030095>

Dufrêne M, Legendre P (1997) Species Assemblages and Indicator Species: the Need for a Flexible Asymmetrical Approach. *Ecological Monographs* 67:345–366. [https://doi.org/10.1890/0012-9615\(1997\)067%255B0345:SAAIST%255D2.0.CO;2](https://doi.org/10.1890/0012-9615(1997)067%255B0345:SAAIST%255D2.0.CO;2)

Escobar ES, Garavito MA, Santacruz SR (2021) Monitoreo de experiencias de restauración ecológica en páramos afectados por plantaciones forestales de *Pinus patula*. Un estudio de caso en el páramo de Rabanal, Boyacá-Colombia. *Biodiversidad en la Práctica* 6:e919–e919. <https://revistas.humboldt.org.co/index.php/BEP/article/view/919>

Espinoza IG, Franco-Gaviria F, Castañeda I, et al (2022) Holocene Fires and Ecological Novelty in the High Colombian Cordillera Oriental. *Front Ecol Evol* 10:. <https://doi.org/10.3389/fevo.2022.895152>

Fernández-Méndez F, Velasco-Salcedo VM, Guerrero-Contecha J, et al (2016) Recuperación ecológica de áreas afectadas por un incendio forestal en la microcuenca Tintales (Boyacá, Colombia). *Colomb For* 19:. <https://doi.org/10.14483/udistrital.jour.colomb.for.2016.2.a02>

Fitzpatrick M, Sanders N, Normand S, et al (2013) Environmental and historical imprints on beta diversity: Insights from variation in rates of species turnover along gradients. *Proceedings Biological sciences / The Royal Society* 280:20131201. <https://doi.org/10.1098/rspb.2013.1201>

Fried G, Carboni M, Mahaut L, Violle C (2019) Functional traits modulate plant community responses to alien plant invasion. *Perspectives in Plant Ecology, Evolution and Systematics* 37:53–63. <https://doi.org/10.1016/j.ppees.2019.02.003>

Fusco EJ, Balch JK, Mahood AL, et al (2022) The human–grass–fire cycle: how people and invasives co-occur to drive fire regimes. *Frontiers in Ecology and the Environment* 20:117–126. <https://doi.org/10.1002/fee.2432>

Galappaththi HSSD, de Silva WAPP, Clavijo McCormick A (2023) A mini-review on the impact of common gorse in its introduced ranges. *Trop Ecol* 64:1–25. <https://doi.org/10.1007/s42965-022-00239-9>

Gallien L, Carboni M (2017) The community ecology of invasive species: where are we and what's next? *Ecography* 40:335–352. <https://doi.org/10.1111/ecog.02446>

Giles AL, Silva MC, Mazzochini GG, et al (2025) Fire triggers reestablishment of invasive grasses in a neotropical savanna under restoration. *Restoration Ecology* 33:e14295. <https://doi.org/10.1111/rec.14295>

Gil-Romera G, Adolf C, Benito BM, et al (2019) Long-term fire resilience of the Ericaceous Belt, Bale Mountains, Ethiopia. *Biol Lett* 15:20190357. <https://doi.org/10.1098/rsbl.2019.0357>

Guclu C, Luk C-L, Ashton LA, et al (2024) Beta diversity subcomponents of plant species turnover and nestedness reveal drivers of community assembly in a regenerating subtropical forest. *Ecology and Evolution* 14:e70233. <https://doi.org/10.1002/ece3.70233>

Hofstede RGM, Llambí LD (2020) Plant Diversity in Páramo—Neotropical High Mountain Humid Grasslands. In: *Encyclopedia of the World's Biomes*. Elsevier, Oxford, pp 362–372

Hsieh TC, Ma KH, Chao A (2016) iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods in Ecology and Evolution* 7:1451–1456. <https://doi.org/10.1111/2041-210X.12613>

Instituto de Hidrología, Meteorología y Estudios Ambientales (IDEAM) (2024) Normales climatológicas del período 1991-2020. Normales climáticas estándar. <https://www.ideam.gov.co/sala-de-prensa/informes/Normales-clim%C3%A1ticas-est%C3%A1ndar?page=0>.

Instituto Geográfico Agustín Codazzi (IGAC) (2001) Mapa Digital de Suelos del Departamento de Cundinamarca, República de Colombia. Escala 1:100.000. Colombia en Mapas, Portal Nacional de Información Geoespacial. <http://www.colombiaenmapas.gov.co/?u=0&t=43&servicio=395>.

Instituto Geográfico Agustín Codazzi (IGAC) (2004) Mapa de Cobertura de la Tierra. Adaptación Corine Land Cover. República de Colombia. Escala 1:100.000. Periodo 2018. Colombia en Mapas, Portal Nacional de Información Geoespacial. <http://www.colombiaenmapas.gov.co/?u=0&t=43&servicio=387>.

Instituto Geográfico Agustín Codazzi (IGAC) (2021) Mapa de Cobertura de la Tierra. Adaptación Corine Land Cover. República de Colombia. Escala 1:100.000. Periodo 2018. Colombia en Mapas, Portal Nacional de Información Geoespacial. <http://www.colombiaenmapas.gov.co/?u=15&t=43&servicio=881>.

Instituto Geográfico Agustín Codazzi (IGAC) (2022) Coberturas de las Tierras Complejo Cruz Verde Sumapaz temporalidad 2019. Estudio Multitemporal de las coberturas y Uso de la Tierra y Levantamiento de Suelos a escala 1:10.000. Colombia en Mapas, Portal Nacional de Información Geoespacial. <http://www.colombiaenmapas.gov.co/?u=25&t=43&servicio=4219>.

Jakovac CC, Meave JA, Bongers F, et al (2022) Strong floristic distinctiveness across Neotropical successional forests. *Science Advances* 8:eabn1767. <https://doi.org/10.1126/sciadv.abn1767>

Jiang L, Zhang X, Zhu J, et al (2023) Environmental heterogeneity determines beta diversity and species turnover for woody plants along an elevation gradient in subtropical forests of China. *FORRES 3*:. <https://doi.org/10.48130/FR-2023-0026>

Jost L, González-Oreja J (2012) Midiendo la diversidad biológica: más allá del índice de Shannon. *Acta Zoologica Lilloana* 56:3–14

Kato-Noguchi H, Kato M (2025) The Impact of Life History Traits and Defensive Abilities on the Invasiveness of *Ulex europaeus* L. *Diversity* 17:805. <https://doi.org/10.3390/d17110805>

Lázaro-Lobo A, Alonso Á, Fernández RD, et al (2023) Impacts of Plant Invasions on Ecosystem Functionality: A Perspective for Ecosystem Health and Ecosystem Services. In: Tripathi S, Bhadouria R, Srivastava P, et al. (eds) *Plant Invasions and Global Climate Change*. Springer Nature, Singapore, pp 31–56

León Cordero R, Torchelsen FP, Overbeck GE, Anand M (2016) Invasive gorse (*Ulex europaeus*, Fabaceae) changes plant community structure in subtropical forest–grassland mosaics of southern Brazil. *Biol Invasions* 18:1629–1643. <https://doi.org/10.1007/s10530-016-1106-5>

Li Z, Wei J, Zhou X, et al (2024) Dynamic restoration mechanism of plant community in the burned area of northeastern margin of Qinghai-Tibet Plateau. *Front Plant Sci* 15:.
<https://doi.org/10.3389/fpls.2024.1368814>

Madrigal J, Marino E, Guijarro M, et al (2012) Evaluation of the flammability of gorse (*Ulex europaeus* L.) managed by prescribed burning. *Annals of Forest Science* 69:387–397.
<https://doi.org/10.1007/s13595-011-0165-0>

Magarik YAS, Roman LA, Henning JG (2020) How should we measure the DBH of multi-stemmed urban trees? *Urban Forestry & Urban Greening* 47:126481.
<https://doi.org/10.1016/j.ufug.2019.126481>

Marino E, Guijarro M, Hernando C, et al (2011) Fire hazard after prescribed burning in a gorse shrubland: Implications for fuel management. *Journal of Environmental Management* 92:1003–1011. <https://doi.org/10.1016/j.jenvman.2010.11.006>

Melnik KO, Valencia A, Katurji M, et al (2024) Effect of live/dead condition, moisture content and particle size on flammability of gorse (*Ulex europaeus*) measured with a cone calorimeter. *Int J Wildland Fire* 33:WF23167. <https://doi.org/10.1071/WF23167>

Moscol Olivera MC, Cleef AM (2009) A phytosociological study of the páramo along two altitudinal transects in El Carchi province, northern Ecuador. *phyto* 39:79–107.
<https://doi.org/10.1127/0340-269X/2009/0039-0079>

Mostacedo B, Fredericksen TS (2000) *Manual de metodos básicos de muestreo y análisis en ecología vegetal*. 87

Murad CA, Pearse J, Huguet C (2024) Multitemporal monitoring of paramos as critical water sources in Central Colombia. *Sci Rep* 14:16706. <https://doi.org/10.1038/s41598-024-67563-z>

Obando-Cabrera L, Díaz-Timoté JJ, Bastarrika A, et al (2025) The Paramo Fire Atlas: quantifying burned area and trends across the Tropical Andes. *Environ Res Lett* 20:054019.
<https://doi.org/10.1088/1748-9326/adc8ba>

Ocampo-Zuleta K, Beltrán-Vargas J (2018) Modelación dinámica de incendios forestales en los Cerros Orientales de Bogotá, Colombia. *Madera y bosques* 24:.
<https://doi.org/10.21829/myb.2018.2431662>

Ocampo-Zuleta K, Parrado-Rosselli Á (2023) Functional diversity in an Andean subpáramo affected by wildfire in Colombia. *Plant Diversity* 45:385–396.
<https://doi.org/10.1016/j.pld.2022.11.007>

Ocampo-Zuleta K, Solorza-Bejarano J (2017) Banco de semillas de retamo espinoso *Ulex europaeus* L. en bordes del matorral invasor en un ecosistema zonal de bosque altoandino, Colombia. *Biota Colombiana* 18:89–98. <https://doi.org/10.21068/c2017.v18s01a05>

Oksanen J (2022) *_vegan: Community Ecology Package_*. R package version 2.6–4

Osinaga O, Baez S, Cuesta F, et al (2014) Monitoreo de diversidad vegetal y carbono en bosques andinos-Protocolo extendido. CONDESAN/IER-UNT/COSUDE, Quito, Ecuador

Pebesma E (2018) The R Journal: Simple Features for R: Standardized Support for Spatial Vector Data. *The R Journal* 10:439–446. <https://doi.org/10.32614/RJ-2018-009>

Pickett STA (1989) Space-for-Time Substitution as an Alternative to Long-Term Studies. In: Likens GE (ed) Long-Term Studies in Ecology: Approaches and Alternatives. Springer, New York, NY, pp 110–135

R Core Team (2026) R: The R Project for Statistical Computing. <https://www.r-project.org/>. Accessed 11 Aug 2026

Ramsay PM, Oxley ERB (1997) The growth form composition of plant communities in the ecuadorian páramos. *Plant Ecology* 131:173–192. <https://doi.org/10.1023/A:1009796224479>

Rangel Churio JO, Velázquez A (1997) Métodos de estudio de la vegetación. In: Rangel Churio JO, Van der Hammen T, Velázquez A, et al. (eds) Colombia diversidad biótica II : Tipos de vegetación en Colombia. Universidad Nacional de Colombia-Instituto de Ciencias Naturales, Instituto de hidrología, Meteorología y estudios Ambientales (IDEAM)-Ministerio del Medio Ambiente, Comité de Investigaciones y Desarrollo Científico-CINDEC.U.N, Academia Colombiana de Ciencias Exactas, Físicas y Naturales, pp 59–87

Roberts J, Florentine S (2021) Biology, distribution and control of the invasive species *Ulex europaeus* (Gorse): A global synthesis of current and future management challenges and research gaps. *Weed Research* 61:272–281. <https://doi.org/10.1111/wre.12491>

Sabogal A (2023) The Paramo Ecosystems. In: Sabogal A (ed) Ecosystem and Species Adaptations in the Andean-Amazonian Region: Traditional Land-Use Systems in Peru. Springer International Publishing, Cham, pp 105–130

Sandoya V, Pauchard A, Cavieres LA (2017) Natives and non-natives plants show different responses to elevation and disturbance on the tropical high Andes of Ecuador. *Ecology and Evolution* 7:7909–7919. <https://doi.org/10.1002/ece3.3270>

Sarmiento L, Llambí LD, Escalona A, Marquez N (2003) Vegetation patterns, regeneration rates and divergence in an old-field succession of the high tropical Andes. *Plant Ecology* 166:145–156. <https://doi.org/10.1023/A:1023262724696>

Sodhi DS, Livingstone SW, Carboni M, Cadotte MW (2019) Plant invasion alters trait composition and diversity across habitats. *Ecology and Evolution* 9:6199–6210. <https://doi.org/10.1002/ece3.5130>

Souza EM de C, Farache FHA, Coelho LFM, et al (2026) High β -diversity in fig wasp communities driven by species turnover in widely distributed Neotropical fig trees. *Oikos* 2026:e11653. <https://doi.org/10.1002/oik.11653>

Stotz GC, Gianoli E, Cahill Jr. JF (2019) Biotic homogenization within and across eight widely distributed grasslands following invasion by *Bromus inermis*. *Ecology* 100:e02717. <https://doi.org/10.1002/ecy.2717>

Tomat-Kelly G, Flory SL (2023) Research gaps limit understanding of invasion-fire cycles. *Biol Invasions* 25:693–711. <https://doi.org/10.1007/s10530-022-02951-y>

Torres I, Parra A, Moreno JM (2022) Effects of spatial distance and woody plant cover on beta diversity point to dispersal limitation as a driver of community assembly during postfire succession in a Mediterranean shrubland. *Ecology and Evolution* 12:e9130. <https://doi.org/10.1002/ece3.9130>

Vargas Ríos O, Premauer J, Cárdenas C de LÁ (2002) Efecto del pastoreo sobre la estructura de la vegetación en un páramo húmedo en Colombia. *Ecotropicos* 15:35–50

Wang Y-Y, Guo K, Liu R-L, et al (2025) Similar alpha yet varied beta functional diversities between invasive and native plant species along an elevational gradient. *NeoBiota* 99:1–18.

<https://doi.org/10.3897/neobiota.99.143495>

White S (2013) Grass páramo as hunter-gatherer landscape. *The Holocene* 23:898–915.

<https://doi.org/10.1177/0959683612471987>

Wyse SV, Perry GLW, Curran TJ (2018) Shoot-Level Flammability of Species Mixtures is Driven by the Most Flammable Species: Implications for Vegetation-Fire Feedbacks Favouring Invasive Species. *Ecosystems* 21:886–900. <https://doi.org/10.1007/s10021-017-0195-z>

Zomer MA, Ramsay PM (2021) Post-fire changes in plant growth form composition and diversity in Andean páramo grassland. *Applied Vegetation Science* 24:e12554.

<https://doi.org/10.1111/avsc.12554>

Zomer MA, Ramsay PM (2018) Espeletia giant rosette plants are reliable biological indicators of time since fire in Andean grasslands. *Plant Ecol* 219:79–88. <https://doi.org/10.1007/s11258-017-0779-x>

Zomer MA, Ramsay PM (2020) The impact of fire intensity on plant growth forms in high-altitude Andean grassland. 2020.04.25.061051

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [SupplementaryMaterial.pdf](#)