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Prescribed burning reshapes ethnobotanically relevant plant communities in continental Mediterranean forests

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Prescribed burning (PB) is widely applied in Mediterranean forests, yet its short-term effects on medicinal plant resources and their potential contribution to cultural ecosystem services remain insufficiently characterised. This study examines how seasonal PBs (spring = early, summer = ecological, autumn = late) influence the availability and functional composition of medicinal understorey species in *Pinus nigra* subsp. *salzmannii* forests at 1,250–1,300 m a.s.l. in the Serranía de Cuenca Mountains (central–eastern Iberian Peninsula). Plant cover and diversity were assessed in 12 plots approximately 1 year after burning, and species were classified according to Raunkiaer life-forms and medicinal uses based on ICD-11 therapeutic categories. In the short term, PB reduced total medicinal plant cover by approximately 35–50%, with stronger declines following early- and ecological burns. These reductions were mainly associated with decreases in phanerophytes and, to a lesser extent, chamaephytes, whereas geophytes and hemicryptophytes showed higher post-fire persistence, particularly after early-season burning. In parallel, ICD categories linked to digestive, dermatological, neurological and genitourinary uses exhibited lower cover in burned plots, while some anti-infective and wound-related categories showed greater short-term resilience. α -diversity declined most strongly after ecological burns, indicating short-term compositional homogenisation. Overall, the results suggest that PB acts as a selective short-term filter on medicinal plant availability, with responses mediated by plant functional traits. By combining functional and therapeutic classifications, this study provides an integrative perspective for interpreting short-term fire effects on medicinal plant assemblages and identifies hypotheses to be tested through longer-term post-fire monitoring.

KEYWORDS

ethnopharmacology, fire ecology, ICD-11therapeutic categories, medicinal plants, Raunkiaer life-forms

1 Introduction

Wildfire regimes worldwide are increasingly shaped by the combined effects of climate change, vegetation dynamics and human activity (Bowman et al., 2009). In continental Mediterranean areas such as the Serranía de Cuenca Mountains, climate-driven projections suggest that shifts in temperature and precipitation regimes are likely to modify fuel

moisture conditions and extend the duration of high fire-weather periods, thereby influencing future fire behaviour and ecosystem responses (Ruffault et al., 2020). These changes are particularly pronounced in the Mediterranean Basin—one of the world's major biodiversity hotspots (Myers et al., 2000) a region characterised by a long-standing socio-ecological relationship with fire (Pausas and Keeley, 2019).

Within this context, prescribed burning (PB) is widely applied as a fuel-reduction tool to mitigate wildfire risk and enhance landscape resilience (Casals et al., 2016). However, the ecological consequences of PB extend beyond its effects on fuel loads and vegetation structure. Mediterranean forests harbour a rich ethnobotanical heritage, and many understorey species are traditionally valued for their medicinal uses and pharmacological potential (Rivera et al., 2005). These plants contribute not only to local healthcare practices but also to biocultural identity, forming an integral component of cultural ecosystem services (Pereira et al., 2021).

Numerous Mediterranean plant taxa contain well-documented bioactive compounds with pharmacological relevance, including antioxidant, antimicrobial, anti-inflammatory and neuroprotective activities. Many of these compounds are associated with herbaceous and woody understorey species commonly occurring in Mediterranean pine woodlands (Ouerfelli et al., 2021; Watroly et al., 2021). Despite this, comparatively less attention has been paid to how PB influences the availability, diversity and functional composition of medicinal plant species, particularly from an integrated ecological and ethno-pharmacological perspective.

To address this gap, the present study integrates fire ecology with ethnopharmacology by classifying documented medicinal uses of plant species according to the International Classification of Diseases, 11th edition (World Health Organization, 2022). This approach enables the linkage of ecological responses—such as changes in plant cover, abundance and functional composition—with therapeutic categories and disease-related functions. By analysing medicinal plant distribution in burned and unburned plots across three seasonal PB windows (early = spring, ecological = summer, late = autumn), we assessed how seasonally distinct PB conditions influence cultural ecosystem services, as reflected by changes in ethnobotanical species diversity and medicinal plant availability in Mediterranean black pine (*Pinus nigra* subsp. *salzmannii*) woodlands. Seasonal variation in prescribed burning can influence both meteorological conditions and fire behaviour, potentially leading to differences in vegetation responses even under controlled management scenarios (Fernandes and Botelho, 2003).

Specifically, we evaluated whether PB alters: (i) the functional composition of plant communities based on Raunkiaer life-forms; (ii) the representation of species associated with different ICD therapeutic categories; and (iii) overall α -diversity indices linked to medicinal resource richness. We hypothesised that ecological burn would produce the strongest short-term declines in medicinal plant diversity and availability (one-year post-fire), particularly within ICD categories dominated by woody taxa (e.g., dermatological, gastrointestinal and neurological uses). Conversely, therapeutic categories associated with fire-resilient life-forms—such as digestive or anti-infective uses linked to geophytes and hemicryptophytes—were expected to exhibit higher short-term recovery following PB.

2 Materials and methods

2.1 Study area

The study was conducted in the Serranía de Cuenca Mountains, near the village of Beteta (Cuenca Province, central Spain), within the Iberian Mountain System. The area is dominated by *Pinus nigra* Arn. subsp. *salzmannii* forests, with an average stand density of $1,281 \pm 256$ trees ha^{-1} , a mean canopy height of 7.25 ± 3.27 m, and an average diameter at breast height (DBH) of 27.4 ± 6.8 cm. The understorey vegetation is composed of typical Mediterranean shrub and herbaceous species, including *Genista scorpius* L., *Arctostaphylos uva-ursi* L., *Juniperus communis* L., *Rosa canina* L., *Amelanchier ovalis* Medik., *Lavandula* spp. and *Thymus* spp.

The centroid of the study area is located at $40^{\circ}33'05.1''\text{N}$, $2^{\circ}06'32.9''\text{W}$ (Figure 1). The terrain ranges from 1,250 to 1,300 m a.s.l., with a gentle mean slope of 4% (± 1.3). According to the Köppen–Geiger climate classification, the region exhibits a temperate Mediterranean climate with dry summers (Csb) (Kottek et al., 2006). Mean annual temperature is 10.2°C , with average minimum and maximum temperatures of 1.7°C and 20.1°C , respectively. Mean annual precipitation is 601 mm, with minimum rainfall occurring in July–August (≈ 10 mm) and a peak in October (≈ 60 mm) (AEMET, 2022; 1990–2020 reference period).

2.2 Experimental design and sampling

A total of twelve square plots (30×30 m) with comparable environmental conditions were established (Supplementary Annex S1). Three plots were assigned to early-season prescribed burning (May 2016), three to late-season burning (October 2017), and three to ecological burning (July 2019). Vegetation surveys were conducted approximately one year after each burn event (2017, 2018 and 2020 respectively) in order to assess short-term post-fire vegetation responses. The remaining three plots were left unburned and served as control (C) plots. Plots were separated by a minimum distance of 100 m to minimise spatial autocorrelation and pseudo-replication (Blaser et al., 2013).

Vegetation responses to prescribed burning were assessed under a short-term post-fire framework. In all burned plots, understorey vegetation was surveyed approximately one year after the corresponding prescribed burn. This time window was selected to capture early post-fire responses while minimising short-term variability associated with immediate post-fire disturbance, as commonly adopted in Mediterranean fire-ecology studies (Pausas, 2004; Pausas and Keeley, 2019). Accordingly, all results presented in this study reflect short-term post-burn effects (≈ 12 months after fire) rather than medium- or long-term recovery dynamics.

Before each PB, a preliminary soil characterisation was conducted in each plot. Soil physico-chemical properties were measured one week before the corresponding burn event to ensure comparable pre-burn conditions across treatments. Subsequent analyses confirmed that these variables did not differ significantly among plots (Supplementary Annex S2).

Long-term climatic conditions were also compared with those recorded during the study period (Supplementary Annex S3). Following the approach of Alizoti et al. (2010), this comparison showed that although total precipitation during 2016–2020 was

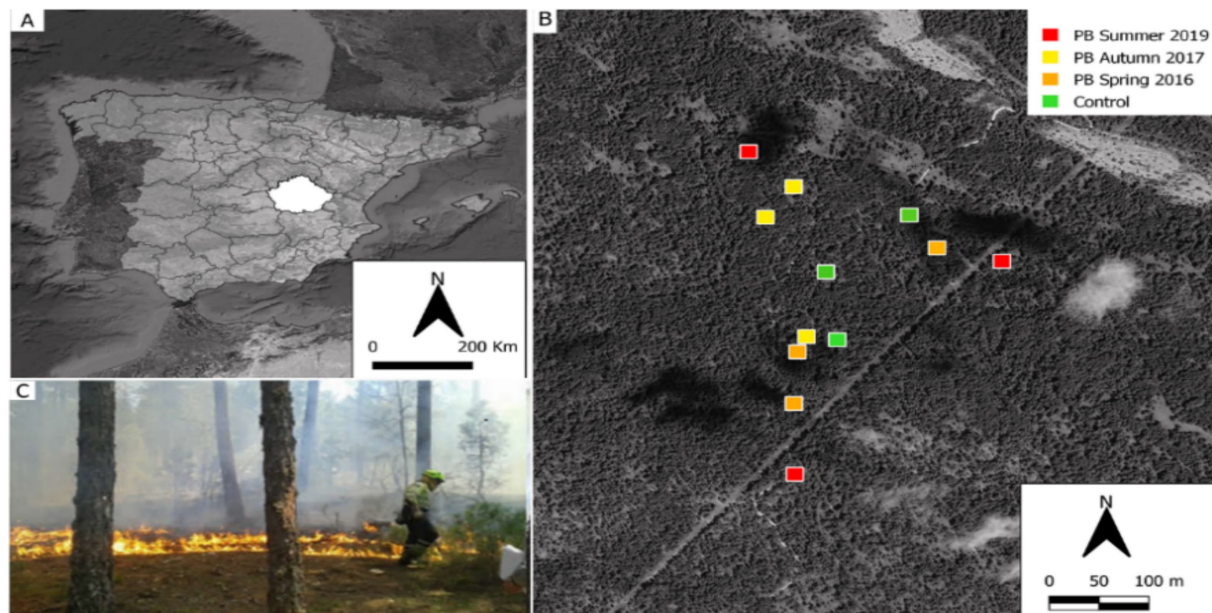


FIGURE 1

(A) Province of Cuenca, Spain. (B) Plots where PBs were applied in summer (ecological = red), plots where PBs were applied in late (late = yellow), plots where PBs were applied in spring (early = orange), and the control plots (unburned = green). (C) Burning an experimental plot.

slightly lower than the long-term average, this deviation affected all plots equally (both control and burned). Consequently, these climatic variations were not expected to introduce differential bias among treatments. Because seasonal PB could not be replicated across multiple years, treatment effects are interpreted as season–treatment combinations rather than independent temporal replicates within a short-term post-fire context.

2.3 Prescribed burning (PB) operations

PBs were implemented using a backfire ignition pattern in all seasons. Ignition was conducted against the predominant wind direction, with fire lines spaced 1 m apart and oriented perpendicularly. This configuration promoted controlled fire propagation with relatively short residence times, thereby limiting soil overheating, convective heat fluxes and extreme temperature peaks, even under warmer seasonal conditions (Vega et al., 2000).

PBs were carried out in different years owing to the narrow, season-specific meteorological windows required for safe implementation. All burns were conducted by certified regional fire-management personnel following standardised operational protocols for Mediterranean PB. Although fire intensity was not formally classified, burns were designed to remain within low-to-moderate operational fire-behaviour ranges. Seasonal differences therefore reflect variation in meteorological context and fuel conditions rather than intentional contrasts in fire intensity.

According to Anderson's (1982) classification, the fuel model corresponded to Model 7 (flammable shrub fuels >1.5 m height). The dominant understorey fuel components included *Genista scorpius* L., *Bromus erectus* Huds., *Ononis spinosa* L. and *Pilosella castellana* Boiss. & Reut. To characterise thermal conditions during combustion, six thermocouples (HOBO UX120 4-Channel Analogue Logger dataloggers) were installed per plot. A total of eighteen dataloggers were distributed across four vertical positions:

2 cm below ground, at the mineral soil surface (0 cm), at the litter layer, and 30 cm above ground.

Fire propagation patterns were consistent with shrub-dominated fuel types and aligned with Spanish technical fire-behaviour models derived from digital terrain and phytoclimatic datasets (MAPAMA, 2022). Meteorological conditions during PB varied among seasons but remained within the operational thresholds established by regional authorities for safe PB execution (Table 1).

Thermocouple data revealed clear seasonal differences in heat exposure, with PB ecological generating the highest temperatures at both the organic layer and 30 cm above-ground sensors, whereas PB early produced the lowest thermal peaks (Table 1). While these measurements provide a detailed characterisation of the thermal environment experienced during combustion, they do not permit a formal classification of fire intensity *sensu stricto*. Standard intensity classifications require additional metrics such as flame length, rate of spread and fuel consumption (Fernandes and Botelho, 2003), which were not recorded in this study.

Accordingly, treatments are interpreted in terms of their measured thermal profiles, residence times and season-specific fuel and meteorological conditions, which together define the fire environment experienced by the understorey vegetation. This approach provides a transparent and empirically supported description of seasonal fire behaviour without inferring intensity classes that cannot be robustly supported by the available data (Knapp et al., 2009).

2.4 Understorey vegetation, ethnobotanical classification and α -diversity

All vegetation measurements were conducted approximately 1 year after each burning in the prescribed-burn plots, ensuring consistency in post-fire assessment timing across seasons. Understorey vegetation was assessed using the line-intercept method (Canfield, 1941), a rapid and widely applied approach for estimating plant cover

TABLE 1 Meteorological conditions and maximum temperatures recorded during seasonal prescribed burns.

Season	Air temperature (°C)	Relative humidity (%)	Wind speed (km/h)	2 cm depth soil surface (°C)	Mineral soil surface (°C)	Organic layer (°C)	30 cm above soil surface (°C)	With temperatures above 100 °C (min)
Early	20	41	3.1	3.1 ± 1.3	28.1 ± 5.2	204.8 ± 11.5	361.7 ± 65.3	1 ± 0.1
Late	18	47	3.2	18 ± 0.8	37.1 ± 5.4	389.7 ± 32.1	702.3 ± 59.6	5 ± 2.1
Ecological	24	37	2.3	26 ± 1.5	68.1 ± 7.1	591.8 ± 21.7	635.9 ± 42.1	15 ± 5.2

Heat residence time above 100 °C occurred primarily in the litter layer and above the soil surface, with limited duration at ground level. These measurements indicate short residence times and moderate thermal exposure experienced by the understorey vegetation, without allowing a formal classification of fire intensity *sensu stricto*.

Values represent mean ± SD.

in heterogeneous Mediterranean environments (Pokswinski et al., 2021). In each plot, three 30-m transects were established at distances of 5 m, 15 m and 25 m from the plot origin. The cumulative linear cover of each vascular plant species intersecting the transect line was recorded.

All identified species were subsequently classified according to Raunkiaer's life-form system including phanerophytes, chamaephytes, hemicryptophytes, geophytes and therophytes. This functional classification was used to interpret vegetation responses to PB, particularly in according to the International Classification of Diseases (World Health Organization, 2022), which groups therapeutic applications by terms of regeneration strategies and post-fire persistence of medicinally relevant taxa.

In parallel, species were assigned to medicinal-use categories following the International Classification of Diseases (World Health Organization, 2022), which groups therapeutic applications according to the targeted body system or pathological condition. The ICD therapeutic categories considered in this study included: infectious diseases (INF), neoplasms (NEO), immune system disorders (IMM), endocrine, nutritional and metabolic diseases (ENDM), mental, behavioural and neurodevelopmental disorders (MENT), diseases of the nervous system (NEU), circulatory system diseases (CIRC), digestive system diseases (DIG), skin diseases (SKIN), diseases of the genitourinary system (GEN), injuries and poisoning (TRAU), and non-medical uses (NMU). The ICD-11 framework was used here as a comparative and functional classification tool to group medicinal uses according to affected body systems, rather than as a direct representation of local ethnomedicinal practices or clinical efficacy. This approach allows the integration of ethnobotanical information into an ecologically interpretable framework while maintaining conceptual separation from biomedical diagnosis.

By integrating Raunkiaer life-forms with ICD therapeutic categories, we linked ecological shifts in vegetation structure to changes in the availability of culturally and pharmacologically relevant plant groups, allowing an eco-pharmacological interpretation of PB effects.

To quantify changes in community structure, α -diversity was calculated for each plot and season using three widely applied indices: Shannon diversity (H'), Pielou's evenness (J) and Simpson diversity (D). All indices were computed using the *vegan* package in R (Oksanen et al., 2015). Species cover values were standardised prior to analysis to ensure comparability across plots and seasons. Diversity indices were calculated as follows:

$$H' = -\sum p_i \ln(p_i) \quad (1)$$

$$D = 1 - \sum p_i^2 \quad (2)$$

$$J = \frac{H'}{\ln(S)} \quad (3)$$

Where p_i represents the proportional cover of species i and S is species richness within each plot.

3 Statistical analyses

All statistical analyses were conducted in R v.4.5.2 (R Core Team, 2022) using RStudio as the development environment. Before modelling, the dataset was screened for outliers, zero inflation and leverage effects.

To evaluate the effects of PB on medicinal plant communities, generalised linear mixed models (GLMMs) were fitted using a Tweedie error distribution with a log link function, which is appropriate for semi-continuous ecological data characterised by right-skewness and a substantial proportion of zeros (Dunn and Smyth, 2005, 2008). Plant cover was used as the response variable. Treatment (control vs. prescribed burn) and season (Early, Ecological, Late) were included as fixed factors (Fernandes and Botelho, 2003; Alizoti et al., 2010).

Three complementary models were fitted to assess different aspects of vegetation response to prescribed burning (Hartig, 2016):

- Total medicinal plant cover: coverage ~ treatment * season
- Functional responses according to Raunkiaer life-forms: coverage ~ treatment * life_form + treatment * season
- Responses according to ICD-11 therapeutic categories: coverage ~ treatment * ICD_category + treatment * season

The full three-way interaction was initially considered but was removed from the final model due to insufficient statistical support and to improve model parsimony.

Because PB were implemented in different years and could not be temporally replicated, the analysis focuses on treatment effects within each seasonal window using model-derived contrasts. For graphical representation and interpretation of effect sizes, back-transformed estimated marginal means ($\pm$ SE) and pairwise contrasts derived from

the GLMM were used (Table 2; Figure 2). Full model outputs and pairwise contrasts are provided in the [Supplementary Annexes S4–S7](#).

This complementary approach enabled quantification of treatment effects within each seasonal window while reducing potential confounding from interannual climatic variability. Differences in α -diversity indices (Shannon diversity H' , Simpson diversity D and Pielou's evenness J) between treatments were analysed using one-way analysis of variance (ANOVA). These analyses were conducted separately for each season to account for the non-replicated temporal structure of the prescribed burns. Diversity indices were calculated using the vegan package in R.

4 Results

4.1 Overall effects of prescribed burning (PB) across seasons

The GLMM evaluating total medicinal plant cover indicated a significant difference between burned and unburned plots ($z = -1.96$, $p = 0.05$). At the time of sampling (≈ 1 year post-burn), burned plots exhibited lower medicinal plant cover than unburned control plots across all seasonal windows (Figure 2).

Back-transformed estimated marginal means indicated that medicinal plant cover in control plots was approximately 35%–50% higher than in burned plots, depending on the season. Pairwise contrasts between control and burned confirmed significant differences in the early and ecological burning seasons, whereas differences in the late season were weaker and not statistically significant, with control/PB ratios ranging from 1.56 to 2.23 (Table 2).

No significant interaction between treatment and season was detected in the global GLMM ($p > 0.5$), indicating that differences between burned and control plots were directionally consistent across seasonal windows.

4.2 Functional responses according to Raunkiaer life-forms

PB was consistently associated with lower cover of woody life-forms, particularly phanerophytes, across all seasons (Table 3). Pairwise contrasts indicated significantly higher cover in control plots compared with burned plots for phanerophytes in early, ecological, and late seasons (all $p < 0.001$). No significant differences between treatments were detected for the remaining Raunkiaer life-forms, including geophytes, hemicryptophytes, and therophytes ($p > 0.05$).

Estimated marginal means for each life-form across treatment-season combinations are shown in Figure 3, while significant treatment contrasts are summarised in Table 3.

4.3 Responses according to ICD medicinal-use classifications

Significant treatment effects were detected in a limited number of ICD therapeutic categories (Table 4). In both early and ecological seasons, control plots showed significantly higher cover than burned plots for genitourinary (GEN), neurological (NEU), and musculoskeletal (NMU) categories (all $p < 0.05$). In the late season, a significant difference was only observed for neurological-related species (NEU),

TABLE 2 Pairwise contrasts [control vs. prescribed burn (PB)] for total plant cover across seasons, based on estimated marginal means (EMMs).

Season	Ratio (control/PB)	SE	z-value	p-value
Early	2.23	0.604	2.957	0.0031
Ecological	1.93	0.520	2.431	0.0151
Late	1.56	0.420	1.656	0.0977

Ratios represent [control/prescribed burn (PB)] estimated marginal means. Values >1 indicate higher cover in control plots, whereas values <1 indicate higher cover in PB plots. Values represent back-transformed estimated marginal means (EMMs $\pm$ SE) derived from the Tweedie GLMM. *The complete code output is provided in [Supplementary Annex S4](#). Model specification: Tweedie GLMM (log link), response variable = total medicinal plant cover; fixed effects = treatment (control vs PB), season (early, ecological, late) and their interaction; random effect = plot.

Ratios >1 indicate higher cover in control plots. Significant p -values (<0.05) are highlighted in bold.

which remained more abundant in control plots. No significant differences between treatments were detected for the remaining ICD categories across seasons ($p > 0.05$).

Estimated marginal means for ICD therapeutic categories across seasons are presented in Figure 4, and significant fixed effects are summarised in Table 4.

4.4 α -diversity responses to prescribed burning (PB)

Significant differences in α -diversity were observed between burned and control plots across seasons, with the strongest contrasts detected after ecological burn (Figure 5). Pielou's evenness (J) differed significantly between treatments ($p = 0.03$; $F = 2.72$), primarily due to lower evenness in burned plots during the ecological season.

Shannon diversity (H') and Simpson diversity (D) were consistently higher in control plots than in burned plots across all seasons (both $p < 0.01$), with the largest differences observed in ecological and late burns (Table 5).

5 Discussion

The present study shows that, under a short-term post-fire framework (~ 1 year after burning), PB, irrespective of the season in which it was applied, was associated with consistent yet functionally selective differences in the composition and cover of plant species of ethnobotanical and pharmacological relevance relative to unburned control plots at the time of sampling.

Geophytes and other bulbous species—such as *Narcissus* spp.—often show enhanced post-fire flowering and rapid recovery in Mediterranean fire-prone ecosystems. This response is widely attributed to the presence of underground storage organs and fire-stimulated phenology (Keeley et al., 2011a; Pausas and Keeley, 2017). These taxa are frequently rich in bioactive compounds, underscoring their importance for medicinal plant resources. In the present study, this pattern was reflected in the significantly higher cover of geophytes observed after early-season PB.

These contrasting responses indicate that PB does not simply reduce medicinal plant availability but rather appears to act as a selective ecological filter that reshapes the functional and pharmacological profile of the understorey. In this study, implications for cultural

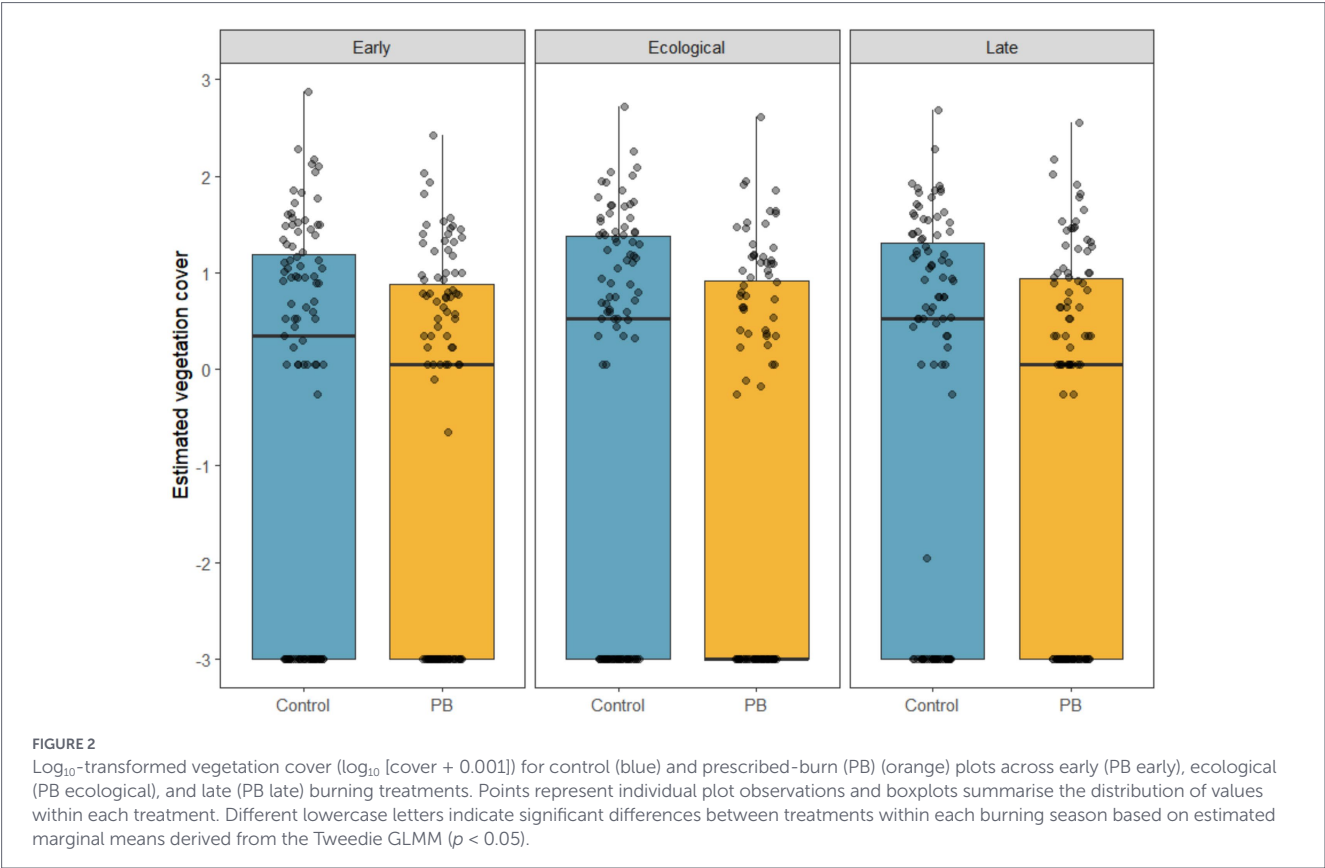


TABLE 3 Estimated marginal means (EMMs ± SE) of plant cover by Raunkiaer life-form, season and treatment derived from the Tweedie GLMM.

Season	Life-form	Control (EMM ± SE)	PB (EMM ± SE)	z-value	p-value	Direction
Early	Phanerophyte	39.46 ± 19.22	8.63 ± 4.91	−2.40	<0.01	↓ PB
Ecological	Phanerophyte	24.32 ± 12.35	5.23 ± 3.17	−2.60	<0.01	↓ PB
Late	Phanerophyte	22.89 ± 11.76	2.73 ± 1.82	−2.31	0.02	↓ PB

Values represent back-transformed estimated marginal means (EMMs ± SE) derived from the Tweedie GLMM. The table reports life-forms for which the control vs. PB contrast was statistically significant according to the model contrast test ($p < 0.05$). EMM values are shown for interpretative purposes, while statistical significance is based on the model-derived contrast (z-test). Non-significant contrasts are reported in the [Supplementary Annex S5](#).

ecosystem services are inferred indirectly through changes in the ecological availability and functional composition of medicinally relevant species, rather than through direct evidence of local use or harvesting practices. From a pharmacological standpoint, these changes are also meaningful because the synthesis and expression of secondary metabolites are tightly linked to plant functional traits, resource-allocation strategies and stress-resilience mechanisms (Wink, 2015; Zandalinas et al., 2022).

Although Raunkiaer life-forms and ICD therapeutic categories originate from distinct conceptual domains—ecological persistence traits versus clinical applications—the integration of both frameworks proved valuable for interpreting the pharmacological consequences of post-fire vegetation restructuring (Moore et al., 2014; Pausas et al., 2018). While shifts in Raunkiaer life-forms following PB have been reported previously in Mediterranean systems, including in nearby forests, the present study extends this knowledge by explicitly linking functional vegetation responses to ICD-based therapeutic categories, thereby providing an applied pharmacological interpretation of post-fire vegetation restructuring (Pausas and Ribeiro, 2017; Huerta et al., 2021). Raunkiaer life-forms determine species’ regenerative mechanisms,

meristem protection and resprouting potential following disturbance while the biosynthesis and ecological deployment of secondary metabolites are strongly mediated by life-history traits, resource-allocation strategies and stress-response mechanisms (Cheynier et al., 2013; Peñuelas and Sardans, 2021). Consequently, declines in phanerophytes after burning translated into reduced availability of woody medicinal taxa traditionally associated with dermatological, neurological or gastrointestinal uses, whereas the resilience of geophytes and hemicryptophytes supported the persistence of species providing anti-inflammatory, digestive or anti-infective properties (Wink, 2015). This integrative ecological–pharmacological perspective therefore offers a robust framework for anticipating how fire-driven vegetation change influences the distribution and accessibility of medicinal plant resources (Kala, 2010).

5.1 Functional shifts and implications for medicinal plant availability

The pronounced decline of phanerophytes—particularly during the PB early and PB ecological treatments—suggests an initial reduction in woody taxa typically characterised by high-molecular-weight

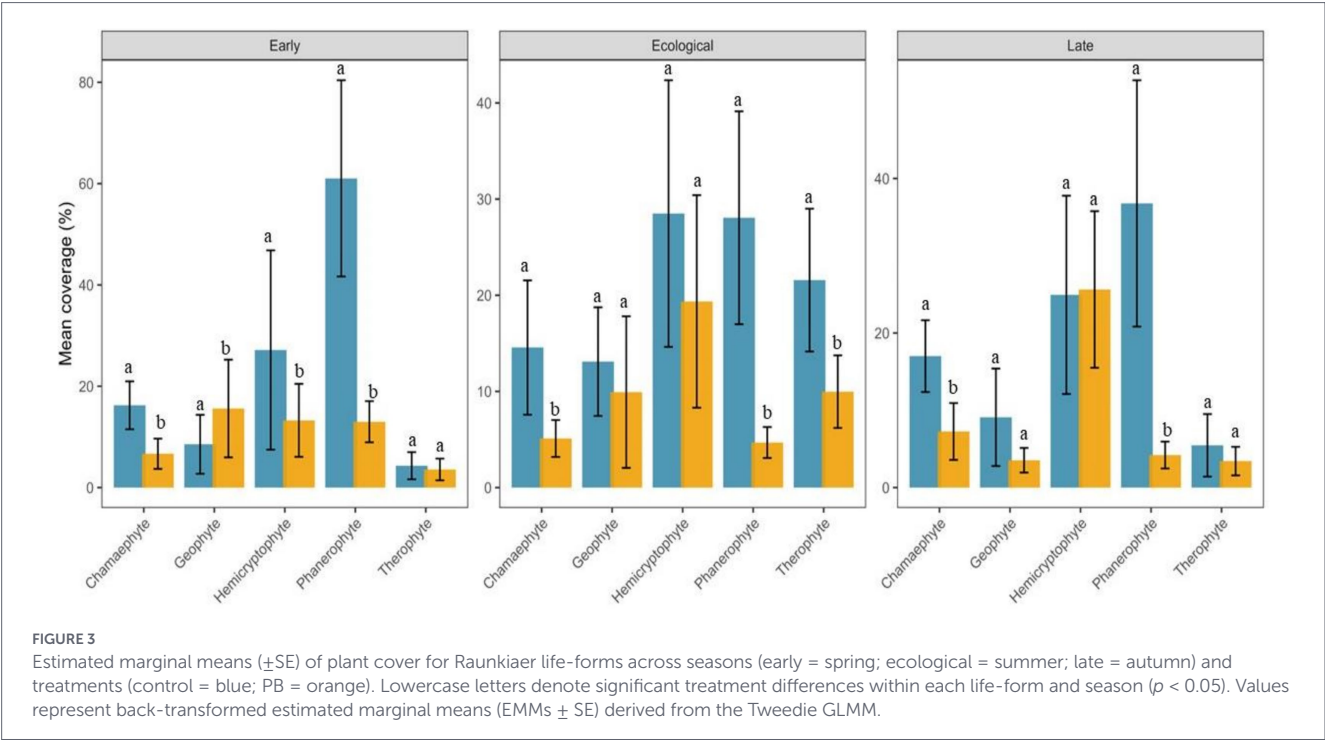


TABLE 4 ICD-11 therapeutic categories showing statistically significant differences in understorey plant cover between control and prescribed burning (PB) plots within each season based on model contrasts ($p < 0.05$).

Season	ICD category	Control (EMM $\pm$ SE)	PB (EMM $\pm$ SE)	z-value	p-value	Direction
Early	GEN	4.70 $\pm$ 6.75	0.96 $\pm$ 1.73	2.10	0.0357	↓ PB
Early	NEU	16.55 $\pm$ 12.05	1.81 $\pm$ 1.76	2.64	0.0082	↓ PB
Early	NMU	7.85 $\pm$ 2.15	4.19 $\pm$ 1.22	2.67	0.0076	↓ PB
Ecological	NEU	6.15 $\pm$ 5.13	3.83 $\pm$ 3.22	2.73	0.0064	↓ PB
Ecological	NMU	8.19 $\pm$ 2.23	3.33 $\pm$ 1.02	2.81	0.0049	↓ PB
Late	NEU	16.89 $\pm$ 12.19	3.25 $\pm$ 2.88	2.32	0.0201	↓ PB
Early	GEN	4.70 $\pm$ 6.75	0.96 $\pm$ 1.73	2.10	0.0357	↓ PB

TERM: ICD categories are treatment groups tested against the reference category (GEN, genitourinary diseases; NEU, diseases of the nervous system; NMU, non-medical use). Only significant control vs PB contrasts are shown. Values represent back-transformed estimated marginal means (EMMs $\pm$ SE) derived from the Tweedie GLMM. Values represent estimated marginal means (EMMs $\pm$ SE) derived from the Tweedie GLMM and are provided for interpretation of treatment effects. Full model outputs and non-significant contrasts are provided in [Supplementary Annex S6](#).

compounds such as alkaloids, diterpenes and condensed tannins, many of which possess well-documented therapeutic properties (Heinrich et al., 2018). This pattern may partly reflect the greater sensitivity of phanerophytic species to fire depending on the seasonal timing of burning. In contrast to other Raunkiaer life-forms, phanerophytes maintain their perennating buds well above the soil surface, leaving meristems and young tissues more exposed to heat damage during fire events (Pausas et al., 2018). When prescribed burning occurs during periods of active growth or reduced carbohydrate reserves, woody species may therefore experience higher physiological stress and lower short-term recovery compared with species possessing protected belowground structures (Pausas and Keeley, 2019; Moreira et al., 2020). Such mechanisms could explain the decline observed in the early post-fire stages of the present study. These results are consistent with previous research indicating that prescribed burning can temporarily reduce the dominance of slow-growing shrubs with chemically complex defence profiles (Keeley et al., 2011a),

thereby altering the short-term availability of plant taxa associated with pharmacologically active secondary metabolites. In contrast, the relative increase or persistence of geophytes and hemicryptophytes following fire aligns with findings from similar Mediterranean ecosystems, where species with underground storage organs or basal meristems exhibit strong post-fire survival and rapid regeneration (Arnan et al., 2007). The protection of regenerative tissues below or close to the soil surface allows these life-forms to withstand moderate fire intensities and quickly exploit the post-disturbance environment characterised by increased light availability and reduced competition. In the present study, geophytes showed a marked increase specifically after the early PB treatment. This pattern may be related to the lower fire intensity and reduced soil heating typically associated with early-season burns, conditions that favour the rapid resprouting of species with underground storage organs while temporarily limiting the recovery of woody competitors (Pausas and Keeley, 2017). In addition, geophytes are often among the first functional

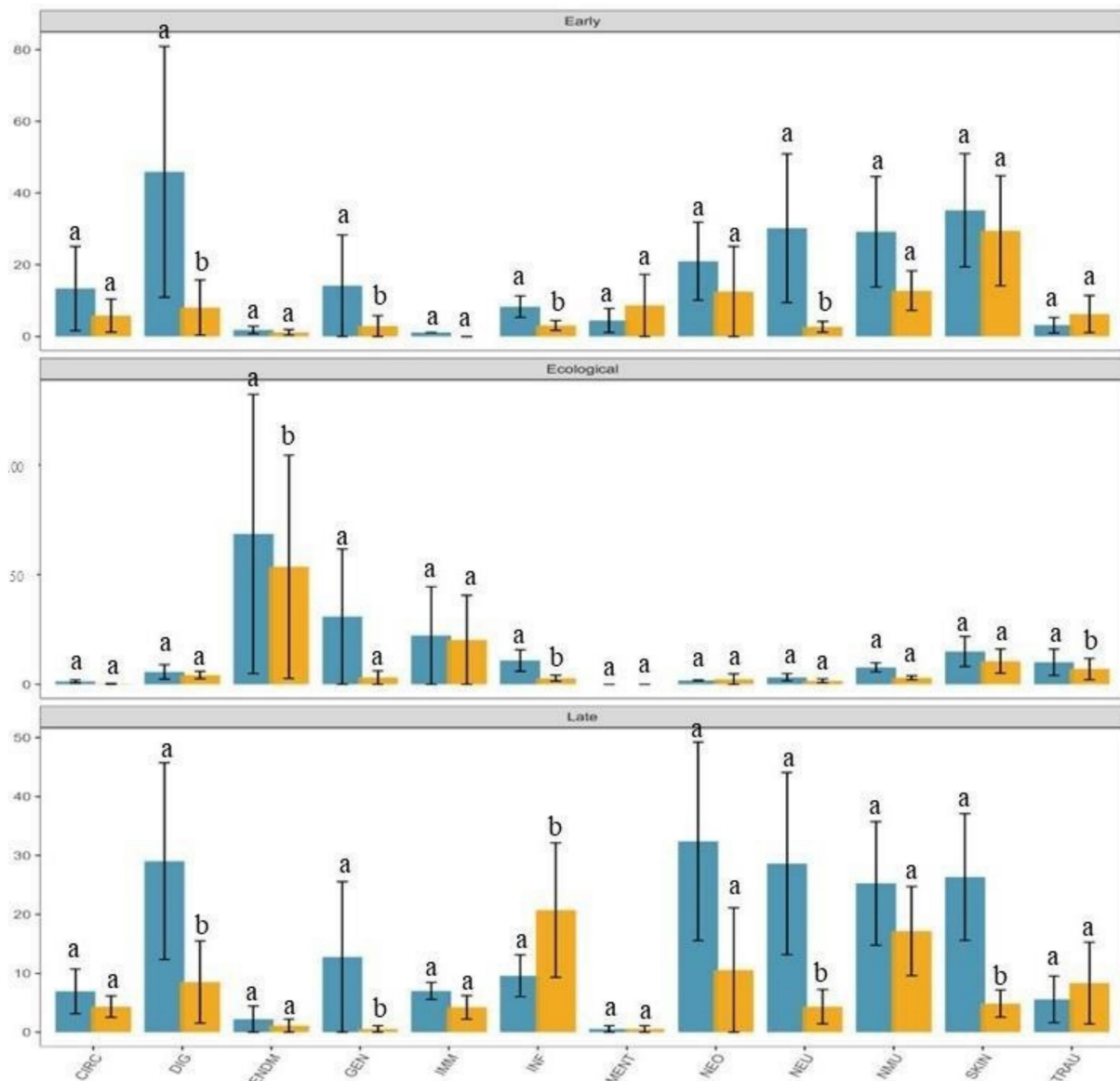


FIGURE 4

Estimated marginal means ($\pm$ SE) of plant cover for ICD therapeutic categories across early, ecological, and late prescribed-burning (PB) seasons. Control plots are shown in blue and PB plots in orange. Lowercase letters indicate significant treatment differences within each ICD category and season ($p < 0.05$). ICD acronyms: CIRC, circulatory system diseases; DIG, digestive system diseases; GEN, diseases of the genitourinary system; NEU, diseases of the nervous system; ENDM, endocrine, nutritional, or metabolic diseases; IMM, immune system diseases; INF, infectious diseases; MENT, mental and neurodevelopmental disorders; NEO, neoplasms; NMU, non-medical use; SKIN, skin diseases; TRAU, trauma and poisoning. Lowercase letters indicate significant treatment differences within each ICD category and season ($p < 0.05$). Values represent back-transformed estimated marginal means (EMMs $\pm$ SE) derived from the Tweedie GLMM.

groups to exploit post-fire resource pulses due to their stored carbohydrate reserves, which allow rapid vegetative growth during the early stages of ecosystem recovery. Many species within these functional groups are also recognised sources of bioactive compounds, including iridoids, saponins, monoterpenes and phenolic derivatives with antioxidant, anti-inflammatory and gastrointestinal activities (Baser and Buchbauer, 2009; Gonçalves et al., 2017). Consequently, the increase in geophytes observed after early PB may temporarily enhance the relative availability of species traditionally used in herbal medicine to treat digestive disorders, inflammatory processes and dermatological conditions (Wink, 2015). These patterns highlight how post-fire shifts in vegetation life-form composition may not only reflect ecological resilience strategies but may also influence the functional pool of medicinal resources available within Mediterranean forest landscapes.

5.2 Impacts on ICD therapeutic categories

The reductions observed in ICD categories such as DIG, GEN, NEU and SKIN during the early- and ecological burns indicate a temporary decline in species associated with gastrointestinal, genitourinary, neurological and dermatological treatments. These categories often include aromatic shrubs and woody taxa rich in essential oils, alkaloids and flavonoids (Santana et al., 2012), compounds that require substantial biomass investment and are frequently sensitive to fire-induced tissue loss. Similar declines in medicinal shrub cover following PB have been reported in Mediterranean and other fire-adapted biomes (Vallejo et al., 2012; Auffret et al., 2024).

By contrast, ICD categories such as IMM, MENT and TRAU showed resilience or even local increases in specific seasons, suggesting

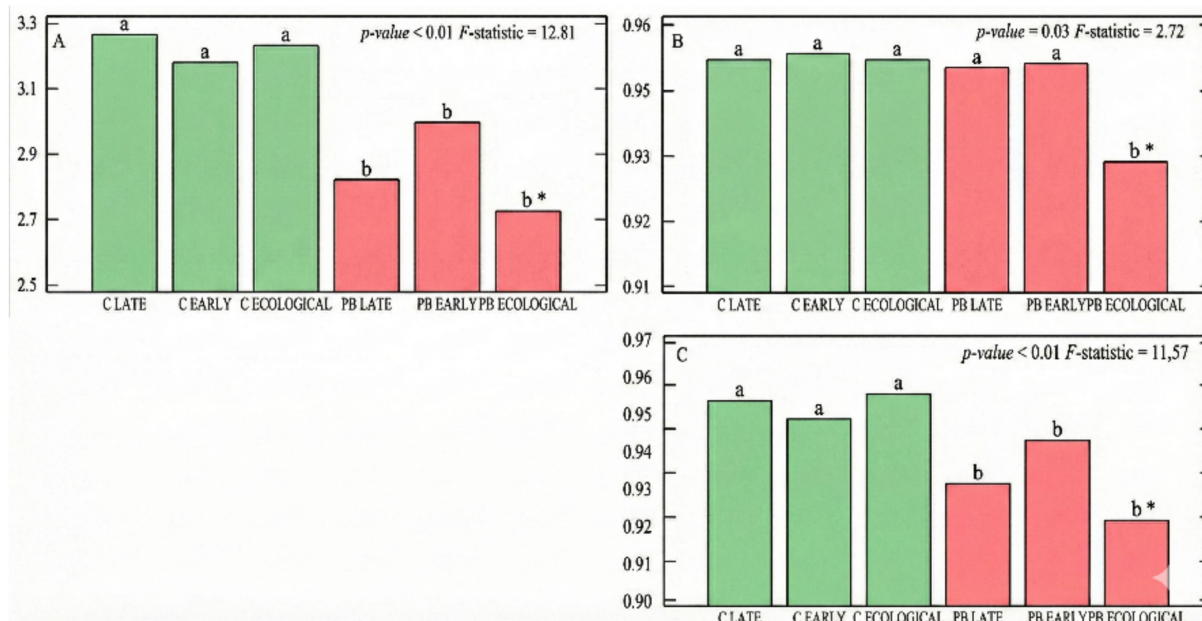


FIGURE 5

α -diversity responses to prescribed burning (PB) across seasons. (A) Shannon diversity (H'), (B) Pielou's evenness (J), and (C) Simpson diversity for control (green) and PB (red) plots. Values represent means $\pm$ SD. Different lowercase letters indicate significant treatment differences within each season based on Tukey *post hoc* tests ($p < 0.05$).

TABLE 5 ANOVA summary for α -diversity indices across seasons and treatments.

Index	Season	df	F	p	Interpretation
Pielou (J)	Ecological	1.10	2.72	0.03	Lower evenness in PB
Shannon (H')	All	1.10	12.81	<0.01	Lower diversity in PB
Simpson (D)	All	1.10	11.57	<0.01	Dominance increase in PB

One-way ANOVA comparing control vs PB plots within each season.

J = Pielou's evenness; H' = Shannon diversity; D = Simpson index. ANOVA was performed independently for each season. Only statistically significant effects ($p < 0.05$) are shown. Complete model outputs are provided in [Supplementary Annex S7](#).

that species producing anti-infective monoterpenes, menthol derivatives or wound-healing phenolics may recolonise or resprout more readily. This pattern is consistent with evidence that many strongly aromatic or anti-infective species possess post-fire germination syndromes or robust resprouting capacities (Bond and Van Wilgen, 1996; Keeley et al., 2011b).

5.3 Seasonality and pharmacological resource dynamics

Although effect sizes varied among seasons, treatment impacts remained directionally consistent, with control/PB ratios ranging between 1.6 and 2.0. This suggests that seasonal timing may modulate the magnitude—but not necessarily the direction—of differences between PB and control plots. Similar patterns have been reported across Mediterranean and other fire-prone ecosystems, where fire exerts a predictable structural influence on plant communities while the magnitude of ecological responses varies with burn timing (Pausas and Verdú, 2008; Silveira et al., 2016).

Importantly, vegetation responses to PB are strongly mediated by plant phenology and fire behaviour, both of which vary seasonally. During spring and early growing seasons, many Mediterranean plants are actively growing and allocating resources to new tissues, which can increase their sensitivity to fire disturbance. Conversely, burns conducted in late summer or autumn may occur under drier fuel conditions and can therefore produce higher fire intensity and more extensive tissue damage (Knapp et al., 2009; Valor et al., 2017). These seasonal differences in plant physiological status and fire behaviour can influence post-fire mortality, resprouting capacity and regeneration dynamics.

In addition to fire behaviour, post-burn climatic conditions likely play an important role in shaping vegetation recovery trajectories. Interannual variability in precipitation and temperature during the first growing seasons following PB can strongly influence germination, resprouting success and competitive dynamics among plant functional groups (Keeley et al., 2011b; Pausas and Keeley, 2017). Consequently, some of the observed differences among burning seasons may partly reflect climatic variability occurring after the burns rather than purely seasonal effects, as post-fire vegetation recovery in Mediterranean ecosystems is strongly mediated by rainfall patterns and climatic conditions during the first years after fire (O'Neill et al., 2017). This reinforces the need to interpret seasonal differences cautiously, as post-fire recovery processes may reflect both burn timing and interannual climatic variability.

5.4 α -diversity and implications for medicinal resource availability

Reductions in α -diversity following PB—particularly during ecological and, to a lesser extent, late burns—indicate that fire not only restructures plant functional groups but also reduces overall community richness and evenness. The significantly lower values of the Shannon (H') and Simpson (D) indices in PB ecological and PB late

treatments suggest a contraction of the dominant taxa pool, consistent with patterns observed in Mediterranean fire-prone systems where dry-season burns promote stronger compositional filtering (Pausas and Keeley, 2017; Moreira et al., 2020).

From a pharmacological perspective, reduced α -diversity may be associated with a narrower range of potential bioactive compounds available within the ecosystem, as suggested by previous studies linking taxonomic and functional plant diversity to phytochemical richness (González-Tejero et al., 2008; Kessler and Kalske, 2018). However, in the absence of direct phytochemical measurements, this relationship should be interpreted as an inference grounded in the literature rather than as an empirical demonstration within the present study. Accordingly, the observed declines in α -diversity are best viewed as indicative of a potential short-term contraction in pharmacological breadth, particularly for ICD categories that showed sensitivity to prescribed burning.

Moreover, the marked decline in evenness (J) under PB ecological conditions indicates that a small number of resilient taxa disproportionately dominate early post-fire stages, potentially narrowing the functional and phytochemical profiles available during recovery. This pattern aligns with previously reported post-fire homogenisation effects in Mediterranean shrublands (Santana et al., 2014) and reinforces the role of fire seasonality in shaping not only species abundance but also the pharmacological landscape of plant communities.

5.5 Implications for medicinal ecosystem services and biocultural resilience

Within the short-term post-fire timeframe assessed in this study, PB not only modifies plant functional composition but also alters the short-term availability of ecosystem services associated with medicinal flora. Medicinal plant harvesting represents a key cultural ecosystem service in many Mediterranean socio-ecological systems. Within the short-term post-fire timeframe assessed in this study, PB not only modifies plant functional composition but also alters the short-term availability of ecosystem services associated with medicinal flora. Medicinal plant harvesting represents a key cultural ecosystem service in many Mediterranean socio-ecological systems (Pereira et al., 2021). The observed declines in phanerophytes and in ICD categories linked to dermatological, gastrointestinal and neurological uses therefore imply a temporary reduction in the availability of plants traditionally valued for these therapeutic functions, particularly woody medicinal taxa with slower post-fire recovery trajectories.

The persistence of geophytes and hemicryptophytes observed in this study indicates that some medicinal ecosystem services may remain functionally buffered in the short term following prescribed burning (Pausas et al., 2018). Because these life forms frequently include species traditionally used for anti-inflammatory, digestive and anti-infective treatments, their stability across treatments may contribute to maintaining part of the pharmacologically relevant plant assemblage after fire (González-Tejero et al., 2008). This resilience likely reflects the protection of regenerative tissues below or close to the soil surface, which limits thermal damage and facilitates rapid post-fire regeneration. Such traits are characteristic of species adapted to recurrent disturbance in Mediterranean ecosystems and may partly explain why these functional groups persisted even where other life forms declined (Gazzaneo et al., 2005; Tavşanoğlu and Pausas, 2018). Importantly, fire seasonality mediates the balance between loss and persistence of these services. Early and ecological burn, which

produced the strongest reductions in α -diversity and medicinal plant cover, may temporarily constrain the multifunctionality of understorey communities. In contrast, PB late resulted in more moderate changes and coincided with the persistence or recovery of geophyte-rich assemblages, suggesting that adjusting burn timing could be explored as a potential management option to help maintain culturally and pharmacologically relevant ecosystem services while still achieving fuel-reduction objectives (Baeza et al., 2002; Knapp et al., 2009).

Overall, these findings emphasise the importance of incorporating cultural ecosystem services into fire-management planning (Valkó et al., 2016). Explicit consideration of the medicinal and biocultural value of plant communities may allow PB programmes to better align ecological resilience, pharmacological resource conservation and local socio-cultural needs.

5.6 Strengths and limitations

This study presents several strengths that enhance its contribution to fire ecology and ethnopharmacology. A key strength lies in the integrative framework combining fire ecology, functional plant traits and pharmacological relevance—an approach still rarely applied in Mediterranean forest ecosystems. By jointly analysing Raunkiaer life-forms and ICD-based therapeutic categories, the study provides a mechanistic interpretation of how PB reshapes not only vegetation structure but also the availability of medicinal resources and associated cultural ecosystem services.

Seasonal PB should therefore be interpreted as a gradient of operational fire conditions rather than discrete intensity classes, consistent with previous work highlighting the role of seasonality in shaping fire effects in Mediterranean ecosystems (Keeley, 2009). An additional and important limitation relates to the temporal structure of the experimental design. PBs were conducted in different years for each seasonal window, reflecting the operational constraints of fire management. Consequently, the observed differences among burning seasons should be interpreted as context-specific season–treatment combinations rather than as purely seasonal effects. Interannual variability in climatic conditions, precipitation patterns and vegetation dynamics may have contributed, at least in part, to the observed responses, and cannot be fully disentangled from burn-season effects in the present study.

The use of generalised linear mixed models with a Tweedie distribution is well suited to the zero-inflated, right-skewed and heteroscedastic nature of plant cover data. The presentation of back-transformed marginal means further enhances the biological interpretability of treatment effects and facilitates comparisons between burned and control plots.

Several limitations should nonetheless be acknowledged. First, plant cover was used as a proxy for medicinal resource availability and does not directly capture post-fire changes in the concentration or composition of bioactive metabolites. Accordingly, strong causal interpretations of seasonal differences should be avoided, and the results are best viewed as short-term responses under specific climatic and operational contexts. Consequently, inferences regarding pharmacological potential should be interpreted with caution. Second, the study focuses on short-term post-burn responses, limiting conclusions about longer-term recovery trajectories of medically important taxa and associated ecosystem services.

An additional conceptual limitation concerns the use of the ICD-11 therapeutic classification. ICD-11 is a biomedical, clinically oriented system, whereas traditional medicinal uses of plants are culturally

mediated, context dependent and often embedded in local knowledge systems. In this study, ICD-11 was not intended to represent or validate local ethnomedicinal practices, but rather to provide a standardised and transferable framework for grouping medicinal uses into functionally comparable categories. This approach facilitates cross-study comparison and ecological interpretation, but it inevitably simplifies the cultural and symbolic dimensions of traditional plant use. While these limitations highlight key avenues for future research—particularly long-term monitoring and post-fire phytochemical analyses—they do not detract from the study's contribution in demonstrating that, under the specific conditions and short-term timeframe assessed, PB functions as a functional and pharmacological filter in Mediterranean pine woodlands. Accordingly, the therapeutic categories analysed should be interpreted as functional proxies rather than as direct indicators of clinical efficacy or culturally specific medicinal practices.

Finally, the absence of direct ethnobotanical data constitutes an additional limitation. While the study evaluates changes in the ecological and pharmacological substrate of medicinal flora, it does not assess the cultural importance, harvesting intensity or actual medicinal use of species by local communities. Therefore, any implications for cultural ecosystem services should be interpreted as potential and context dependent, and future studies integrating ecological monitoring with ethnobotanical fieldwork are needed to fully capture the socio-cultural dimensions of PB.

6 Conclusion

This study shows that PB is associated with consistent short-term shifts in the cover and functional composition of medicinal plant species in Mediterranean pine woodlands. Approximately one year after burning, medicinal plant cover was lower in burned plots across all seasons, with the most pronounced reductions affecting phanerophytes and ICD categories associated with dermatological, gastrointestinal and neurological uses. In contrast, geophytes and hemicryptophytes—life-forms characterised by protected belowground organs—displayed greater short-term persistence and, in some cases, higher representation.

By jointly analysing Raunkiaer life-forms and ICD therapeutic categories, this work highlights how plant functional traits mediate short-term changes in the availability of medicinal resources following fire. Seasonal timing influenced the magnitude of these responses, with early and ecological burns producing stronger short-term effects on medicinal plant cover and α -diversity.

The implications discussed for cultural ecosystem services should therefore be understood as potential and context-dependent, reflecting changes in the ecological and pharmacological substrate of medicinal flora rather than documented patterns of human use. Integrating ecological monitoring with ethnobotanical fieldwork represents a necessary next step to fully assess the socio-cultural dimensions of prescribed burning in Mediterranean forest landscapes.

Accordingly, management implications derived from this study should be interpreted within a short-term ecological response framework and evaluated through longer-term monitoring before being translated into operational fire-management guidelines. Overall, the results suggest that prescribed burning may temporarily modify the composition of medicinal plant assemblages and their potential contribution to cultural ecosystem services. These findings provide a basis for formulating hypotheses on how burn timing could influence medicinal resource availability over longer time frames. Future studies incorporating longer-term vegetation recovery, phytochemical

analyses and socio-cultural dimensions will be necessary to evaluate the persistence of these patterns and their relevance for fire management and conservation planning in Mediterranean landscapes.

Data availability statement

The original contributions presented in the study are included in the article/[Supplementary material](#), further inquiries can be directed to the corresponding author.

Author contributions

ÁF-C: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. DM: Conceptualization, Investigation, Methodology, Project administration, Supervision, Validation, Writing – review & editing. PP-Á: Investigation, Methodology, Validation, Writing – review & editing. JG-R: Investigation, Methodology, Supervision, Validation, Writing – review & editing. JH: Conceptualization, Funding acquisition, Project administration, Resources, Supervision, Validation, Writing – review & editing.

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Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/ffgc.2026.1772327/full#supplementary-material>

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