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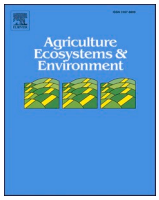

# Effects of multi-scale drivers on plant diversity and forage quality in traditional wood-pastures of Transylvania (Romania)

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ABSTRACT

Traditional wood-pastures are agroforestry systems shaped by long-term low-intensity management. However, the relative importance of drivers of plant diversity and forage quality operating at different spatial scales in these systems remains poorly understood. We investigated 30 traditional wood-pasture sites in Transylvania (Romania) by integrating drivers i) at the large-scale: historical Corona satellite imagery from 1964, contemporary land-cover data, and CHELSA climatic data; ii) at the intermediate-scale: tree and woody configuration; and iii) at the fine-scale: soil surveys. We evaluated the interaction among landscape structure, site factors, plant diversity and forage quality. We analysed long-term changes in land use and woody cover across multiple spatial scales within wood-pasture mosaics. Using linear models and variation partitioning, we assessed the multi-scale environmental determinants on plant taxonomic and functional diversity, and forage quality of the wood-pastures. Landscape composition remained largely stable over six decades, although woody cover declined at most sites, indicating fine-scale structural change within a persistent land-cover mosaic. Climatic conditions such as annual precipitation was positively associated with forage quality and functional richness of specific leaf area, while mean annual temperature and pasture loss were negatively associated with functional richness of plant height. Current forest cover was related to functional richness related to leaf economics and seed mass, whereas soil carbon showed a positive relationship with species richness and leaf-trait diversity. Woody cover was linked to higher species richness but lower forage quality, suggesting a structural trade-off between biodiversity and palatability. Current land use explained the largest proportion of variation in forage quality and species richness, whereas climate and land-use change were more strongly associated with functional composition. These results support hierarchical environmental filtering, whereby regional climate and local habitat structure constrain community assembly more strongly than landscape composition. Our findings about this traditional multi-functional landscape highlight that conserving and restoring wood-pasture functionality requires combined management practices that optimise woody cover, grazing intensity, and soil quality.

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## 1. Introduction

Traditional wood-pastures are among the most distinctive components of Europe's cultural landscapes, shaped by centuries or even millennia of low-intensity management combining livestock grazing, solitary tree maintenance, and in some regions, hay production within the same land-use system (Hartel and Plieninger, 2014; Rotherham, 2015). These semi-natural systems form fine-scale mosaics of open grasslands and scattered trees, generating structural and microhabitat heterogeneity that supports high biodiversity while providing forage and multiple ecosystem services (Manning et al., 2006; Bergmeier et al., 2010). They are among those agroforestry systems of highest ecological and cultural value in Europe, hosting species dependent on both woodland and open habitats (Hartel and Plieninger, 2014; Le et al., 2025a). Beyond their high conservation value, traditional wood-pastures are multifunctional systems managed to provide forage, support extensive livestock production, and maintain long-term ecological functioning. In addition to their biodiversity importance, these landscapes deliver vital ecosystem services and sustain local cultural identity (Plieninger et al., 2015). However, traditional management systems practices have declined across Europe due to rural depopulation, mechanisation, and agricultural intensification (Bugalho et al., 2011; Fischer et al., 2012; Zerbe, 2022). As these ongoing processes persist, wood-pastures are increasingly abandoned, converted, or simplified, threatening biodiversity and their cultural heritage (Bergmeier et al., 2010; Hartel et al., 2013; Roellig et al., 2016; Culbert et al., 2017).

Over the past decades, wood-pastures across Europe have been transformed by profound land-use changes. In much of Western and Central Europe, agricultural intensification through increased fertiliser use, mechanisation, and field enlargement has gradually reduced the fine-scale diversity of traditional landscapes (Chamberlain and Siriwardena., 2000; Geiger et al., 2010; Zerbe, 2022; Neumann et al., 2025). By contrast, Eastern Europe followed a different trajectory: during the mid-twentieth century, land management was reorganised and often intensified (De Moor et al., 2002; Lerman et al., 2004; Hartvigsen, 2014), while the transformations of the 1990s and early 2000s led to rapid privatisation, fragmentation, and widespread land abandonment (Kuemmerle et al., 2008; Culbert et al., 2017; Janišová et al., 2024). As a result, many wood-pastures now undergo accelerated natural reforestation and structural simplification, with declining open habitats and reduction in grassland specialist species (Öllerer., 2014; Jakobsson et al., 2020; Munteanu et al., 2024; Novák et al., 2024). These distinct historical pathways emphasise the consideration of regional land-use legacies for interpreting current biodiversity patterns and guiding conservation and restoration of Europe's wood-pasture systems (Lindenmayer, 2017; Moreno et al., 2018; Zerbe, 2022).

Plant community assembly in wood-pastures is shaped not only by management practices, but also by multiple factors operating at different spatial scales (Götzenberger et al., 2012; Gross et al., 2013; Bricca et al., 2025). At the large spatial scale, regional climatic conditions constrain the regional species pool through temperature and water availability (Woodward and Williams, 1987; de Bello et al., 2013). At the intermediate scale, individual trees and local woody cover act as key structural elements shaping understory biodiversity by creating microhabitat gradients that influence plant diversity and functional composition (Tölgyesi et al., 2018; Padullés Cubino et al., 2021; Bricca et al., 2025). The transition from shaded canopy zones to open grasslands modifies microclimatic and edaphic conditions, increasing soil moisture and organic matter while buffering temperature extremes, particularly at fine spatial scales (Manning et al., 2006; Erdős et al., 2024; Lőrincz et al., 2024). These changes in soil properties likewise play a central role in determining local plant community composition and diversity (Cousins., 2009; Perring et al., 2016; Midolo et al., 2025). As a consequence, strong species turnover may occur over short spatial distances in response to fine-scale soil heterogeneity (Bricca et al., 2023; Le et al., 2025b).

Importantly, historical land-use intensification, such as fertilisation or cultivation, can modify soil fertility and nutrient cycling, creating indirect pathways through which land-use change affects biodiversity. Fertilisation may favour nitrophilous species and reshape plants-soil interactions (Hu et al., 2021; De Long et al., 2023). In wood-pastures, interactions among trees, grazing animals, and topography generate additional soil heterogeneity, which can buffer the ecological effects of land-use change depending on the spatial scale and management intensity (Bruun et al., 2001; Vitali et al., 2025). Linking soil variability with land-use legacies, thus, may provide a more integrated understanding of how abiotic (soil) and biotic (plants) components of cultural landscapes respond to historical and contemporary human pressures.

Despite growing evidence that biodiversity patterns emerge from hierarchical environmental filtering, most studies on wood-pastures relate taxonomic diversity, functional diversity, or forage quality to single land-use descriptors or individual spatial scales (e.g., Graham et al., 2019; Midolo et al., 2025; Rosa et al., 2025). Yet forage quality represents a key ecosystem function in grazed wood-pastures and may respond strongly to changes in vegetation structure and plant functional composition. For example, woody cover and canopy structure can affect forage quality through microclimatic and compositional shifts, with understory vegetation frequently exhibiting higher crude protein content and digestibility than open grasslands (Bernardi et al., 2016; Ripamonti et al., 2025). Consequently, the relative importance and interaction of climate, vegetation structure, soil properties, and landscape-scale land-use change in shaping plant functional composition remain poorly understood, particularly in long-managed cultural landscapes. Multi-scale approaches are therefore needed to clarify how processes operating at different spatial levels jointly structure plant communities and ecosystem functions.

In this study, we integrated historical land-use data, climatic variables (large-scale), woody cover (intermediate-scale), and soil properties (fine-scale) across traditional wood-pastures in Transylvania, Romania. Plant taxonomic and functional diversity were assessed at the fine-scale vegetation plots aggregated at the site level, whereas environmental predictors were quantified across multiple spatial scales. We tested the hypothesis that large-scale (land-use change) exerts a weaker impact on plant functional composition than at fine- and intermediate-scale environmental filters (climate, woody cover, and soil properties). Specifically, we addressed the following research questions:

1) How has land-use composition and woody cover changed over the past 60 years?
2) What is the effect and the relative contribution of historical land-use change, climatic conditions, woody cover, and soil properties in influencing taxonomic diversity, functional diversity, and forage quality?

## 2. Methods

### 2.1. Study area

In our study area in Transylvania (Romania), traditional wood-pastures are widespread. Those wood-pastures are dominated by oak species (*Quercus robur* and *Quercus petraea*) and support diverse plant assemblages associated with semi-natural dry grasslands and open oak woodlands, including communities of classes *Festuco-Brometea* and *Molinio-Arrhenatheretea*, and harbouring species of Pontic, Balkan, and endemic origin (Ţucra et al., 1987; Doniţă et al., 2005; Coldea et al., 2012; Dengler et al., 2012). The study area of approximately 100 km × 60 km spans multiple counties in the southern Carpathians (Fig. 1), with elevations from 300 to 700 m a.s.l. The study area experiences a subcontinental-temperate climate (Rivas–Martínez et al., 2004; Le et al., 2025b). Mean annual temperatures range between 6 and 9 °C, and mean

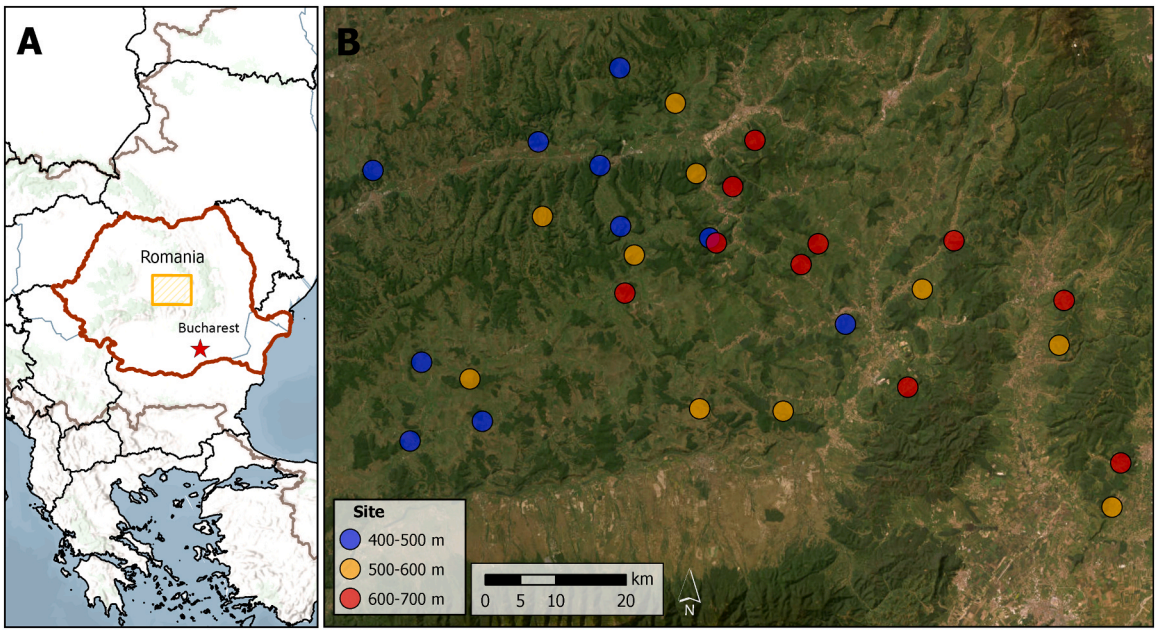


**Fig. 1.** Study area (A) in Romania, and (B) the location of sampling sites in different altitudinal classes in the hills of Transylvania.

annual precipitation varies from 570 to 620 mm (Brun et al., 2022). The vegetation is characterised by a mosaic of scattered trees, shrubs, and herbaceous species typical of mesic to xeric conditions (Ruprecht et al., 2009; Dengler et al., 2012; Le et al., 2025b). Soils in the study sites were Luvisols, Fluvisols, Phaeozems, and Regosols, underlain by Pliocene- to Miocene-age volcanic and sedimentary parent materials, dominantly claystone, sandstone, marl, dacitic and andesitic tuffs, and conglomerates (Finke and Montanarella., 2001). Geographic coordinates and basic characteristics of all study sites are given in Appendix S1.

In Transylvania, traditional wood-pastures typically have low to intermediate tree densities (5–30 mature trees per hectare), with veteran trees scattered rather than forming closed canopies (Hartel et al., 2013; Plieninger et al., 2015). Since the 13th century, Saxon settlements implemented a system of arable fields, hay meadows, forests, and communal wood-pastures, with livestock grazing regulated collectively and veteran trees maintained as long-lived structural elements (Hartel et al., 2015). These management practices persisted through the medieval, early modern, and Austro–Hungarian periods, stabilising land use and creating a structurally diverse landscape that supported high biodiversity (Hartel et al., 2013; Molnár et al., 2015). In the 20th century, Romania, like other Eastern European countries, experienced collectivisation, namely the reorganisation of agriculture, intensified grazing, and promoted logging, reducing veteran tree densities and structural heterogeneity (Micu, 2010; Sutcliffe et al., 2013; Mikulcak et al., 2015; Petrişor and Petrişor, 2017). After 1989, land restitution and rural depopulation triggered differing trajectories, with abandonment and woody encroachment in some areas and the persistence or reactivation of grazing elsewhere (Munteanu et al., 2016, 2024; Feurdean et al., 2017). Since Romania's EU accession in 2007, Common Agricultural Policy (CAP) instruments and agri-environmental schemes have reshaped wood-pasture management in Transylvania by reactivating grazing on previously abandoned pastures. However, they favoured sheep-dominated grazing through subsidy and market incentives, rather than the historically diverse, multi-livestock grazing comprising cattle and buffalo from the 18th century onward and pigs since at least the 16th century (Hartel and Moga, 2010; Sutcliffe et al., 2013; Hartel et al., 2015; Loos et al., 2015). Over the past, only a fraction of pastures and wood-pastures had remained continuously, producing land-use legacies that continue to influence vegetation composition, soil properties, and ecosystem functioning (Foster et al., 2003; Hermy and Verheyen, 2007; Feurdean et al., 2017).

### 2.2. *Vegetation sampling and data preparation*

Vegetation data were collected from traditional wood-pastures in Southern Transylvania (Le et al., 2025b). The study sites are traditionally managed wood-pastures under extensive livestock grazing. Grazing is mainly provided by sheep, cattle, goats, buffaloes, and horses, with most livestock grazing between April and October, while sheep often graze year-round. In the study region, grazing intensity is typically around 7–10 livestock $ha^{-1}$ (Le et al., 2025b). Thirty sites representing traditional wood-pastures were selected using stratified random sampling across three elevation classes (400–500 m a.s.l., 500–600 m a.s.l., and 600–700 m a.s.l.), with one veteran oak tree (*Quercus robur* or *Quercus petraea*), with a diameter at breast height (DBH) $> 75$ cm. At each tree, three 1 m $\times$ 1 m plots were established along a transect starting from the trunk and moving across the canopy edge to outside the canopy with 6–10 m spacing between plots, depending on the extent of the tree canopy. To standardise environmental variation, particularly microclimate and fine-scale gradients, we focused on south-facing plots, as edge orientation strongly affects microclimatic conditions and herbaceous vegetation. We sampled 30 solitary trees with 90 plots on the southern side, ensuring comparable microclimatic conditions across all sites (Fig. 1).

In each plot, all vascular plants were identified to the species level, and cover was visually estimated as a percentage per species. Functional traits belonging to the leaf-height-seed (LHS) scheme, namely plant height (H), specific leaf area (SLA) (Westoby, 1998; Carmona et al., 2021), were collected from FloraVeg.EU database (Chytrý et al., 2024) and seed mass (SM) were collected from Royal Botanic Gardens Kew, Seed Information Database (Seed Information Database (SID), 2023). As all plots had over 80% cumulative cover of species with available quantitative trait data (LHS scheme), trait imputation was not necessary. Trait values were $\log_{10}$–transformed to approximate normal distributions.

### 2.3. Climatic data

Climatic predictors were obtained from the CHELSA dataset at 1-km resolution (Karger et al., 2021). To capture major climatic constraints on vegetation patterns, we extracted mean annual air temperature (bio1, °C), temperature seasonality (bio4, °C/100), annual precipitation (bio12, mm $m^{-2}$ $year^{-1}$), and precipitation seasonality (bio15, kg $m^{-2}$). Besides, we used the De Martonne aridity index, calculated as: $AI = \frac{P}{T+10}$, where $P$ is the mean annual precipitation (mm), and $T$ is the mean annual temperature (°C).

## 3. Land-use data

### 3.1. Large-scale land use

Historical land use was processed using high-resolution Corona satellite imagery from 1964, providing a record of mid 20th century landscape patterns (Munteanu et al., 2024; Rizayeva et al., 2025). Contemporary land cover was characterised using 2024 satellite imagery (Google) and the CORINE Land Cover dataset (CLC 2020_20u1; 25 ha resolution, ≤10 m geometric accuracy, Sentinel–2) (Copernicus Land Monitoring Service CLC et al., 2025). For both time periods, land cover was assessed within a 1-km radius buffer around each sampled tree, processed using QGIS 3.42.0 (QGIS Development Team., 2025). Subsets of Corona images were orthorectified, and the 2024 CORINE polygons served as an initial reference for defining land-use classes. Boundaries were refined through visual photo interpretation, and additional Google Earth imagery was consulted when contemporary land-use classification was uncertain. Historical boundaries of 1964 were reconstructed by adjusting the 2024 polygons based on the Corona imagery, retaining polygon geometry or class assignments when 1964 interpretation was unclear, to minimise inconsistencies from differences in spatial resolution and image clarity. Land-use classes were grouped into three categories, i.e., arable, forest, and pasture (Appendix S2.1).

For the quantitative analysis, CORINE rasters, which were manually adjusted to better reflect land-use types, were clipped to 1-km buffers around each sampling tree in QGIS and reclassified into three aggregated land-cover groups (Appendix S2.2) using the *Raster Calculator*. Each site raster was separated and processed in batch mode to generate unique value reports, from which the proportional cover of each land-cover group within the buffer was calculated. We used these data to compute landscape heterogeneity for each site by applying the Shannon diversity index.

### 3.2. Intermediate-scale woody cover

Woody cover was quantified within a 100 m radius around each sampling tree using historical Corona imagery (1964) and contemporary high-resolution satellite imagery (2024). Woody or non-woody areas were manually delineated in QGIS based on visual interpretation of trees and/or shrubs. The proportion of woody cover within each buffer was then calculated as the percentage of the buffer area occupied by woody vegetation

### 3.3. Soil data

Soil samples were collected from all vegetation plots mentioned above. Following the SIGNAL's project protocol (SIGNAL, 2021), an additional soil plot was established at 24 m from the tree trunk. In our analyses, soil samples from the 2 outside-canopy plots (7 m and 24 m) were merged and considered as a single reference category, as both plots were located beyond the canopy and exhibited similar conditions. Soil pits were dug at each plot to a depth of 60 cm, and were sampled vertically at three depths (0–5 cm, 5–25 cm, 25–40 cm). The topsoil (0–5 cm) was collected using a shovel, whereas the deeper soil layers (5–25 cm and 25–45 cm) were sampled using steel cylinders (98.56 $cm^3$), with four cylinders collected per depth. In 3 sites, dense oak roots limited the depth achieved to 25 cm. In total, 357 soil samples were collected from 120 soil profiles.

All soil samples were air-dried for 15 days, then oven-dried at 40 °C, sieved (2 mm), and milled for analysis. Total carbon and nitrogen were measured with a CHNS Elemental Analyser, and pH was determined in a 1:5 soil-to-water ratio following ISO 10390 (International Organization for Standardization (ISO), 2005). Organic carbon was measured in all samples, and samples with pH > 6.5 were also analysed for inorganic carbon. Bulk density was calculated for the two depths, 5–25 cm and 25–45 cm depth intervals using the dry soil mass (at 105 °C) from the steel cylinders with a volume of 394.24 $cm^3$ . For statistical analyses, soil variables were calculated as mean values across sampling depths and sampling positions to represent overall site-level soil conditions. Distances 1 and 3 m from the tree were combined into a single under-canopy category, whereas samples from 7 m to 24 m were retained separately before calculating the overall site means. To assess the effect of soil sampling depth, all analyses were also repeated using only shallow soil variables (0–5 cm), the results were compared with those from the averaged soil profile using AICc (Appendix S5). Plant communities comprise species with contrasting rooting depths and belowground strategies (Bakker et al., 2021; Klimešová et al. 2021), and the averaged soil profile generally provided stronger model support.

### 3.4. Data integration and analysis

Preliminarily, we aggregated plant species data at the site level by merging the three plots within each site. This aggregation was necessary because the spatial predictors operate at a broader scale and cannot be resolved at the plot level. We expressed the taxonomic diversity with the species richness (SR) and the functional diversity with the functional richness (FRic). Functional richness reflects the range of functional trait values within the plant community (Cornwell et al., 2006; Mason et al., 2013). Both species richness and functional richness provide significant explanatory power when examining the connections between biodiversity and environmental drivers (Liu et al., 2024; Bricca et al., 2025). We calculated SR and FRic for each single trait ($FRic_H$, $FRic_{SLA}$ and $FRic_{SM}$; Villéger et al., 2008). Functional indices were calculated using Gower distance (Pavoine et al., 2009). Additionally, forage quality was quantified using the grassland forage quality index (QI), a standard metric used in grassland management. The index was calculated as: $QI = \Sigma(pi \times qi/5)$, where $pi$ is the proportional cover (%) of species $i$ in the plot, and $qi$ is the forage value assigned to species $i$. Forage values ranged from 0 to 5, where 0 corresponds to species without forage value (X in Kovács, 1979) and 5 represents the highest forage value. The QI was calculated for each site as the cover-weighted average forage value of all recorded species. Based on QI values, grasslands were classified as degraded (0–5%), very poor (5–15%), poor (15–25%), average (25–50%), good (50–75%), and very good (75–100%) (Kovács, 1979).

We selected a set of environmental predictors to test the effects of historical land use, and current land-use composition (arable, forest, pasture, woody cover, landscape heterogeneity (Shannon index)), climatic variables (aridity, bio1, bio4, bio12, bio15, fcf, scd), and soil conditions (bulk density, total carbon content (C), total nitrogen content (N), C:N, pH).

To assess temporal changes in landscape composition between 1964 and 2024, paired *t*-tests were performed for arable land, forest cover, and pasture cover. Additionally, to reduce the number of predictors and select the most important one for each set of variables, we ran separate principal component analysis (PCA) for each group, and selected variables that associated more strongly with PCA axis 1 and PCA axis 2. This resulted in eight variables: for climatic variables we selected mean annual temperature (PC axis 1) and annual precipitation amount (PC axis 2) (Appendix S3.1); for historical land-use changes, pasture change (PC axis 1) and forest change (PC axis 2) (Appendix S3.2); for current


**Fig. 2.** Chord diagram illustrating land-cover transitions between 1964 and 2024; flows connect land-cover groups in 1964 (bottom half) with their corresponding categories in 2024 (top half); ribbon widths are proportional to the area changed from one land-cover type to another.

land-use composition, current forest cover (PC axis 1) and landscape heterogeneity (Shannon index) (PC axis 2) (Appendix S3.3); for soil conditions, soil carbon content (PC axis 1) and C:N content (PC axis 2) (Appendix S3.4). In addition, woody cover was included as a separate predictor because it represents an ecologically important structural component of wood-pastures that influences microclimate, habitat heterogeneity, and understory plant diversity (Manning et al., 2006; Tölgyesi et al., 2018). We examined how the selected environmental variables influence SR and FRic, and QI. For each biodiversity index (SR, FRic, and QI), we first fitted a global linear model using the ordinary least squares regression *lm()* function, including all selected predictors:

*Index* ~ *temperature* + *precipitation* + *current forest cover* + *landscape heterogeneity* + *current woody cover* + *pasture change* + *forest change-* + *soil carbon* + *C:N*.

We then performed model selection using the *dredge* function, ranking models by AICc (Barton, 2023). The best-supported models (lowest AICc value) for each response variable were extracted and summarised to identify the most influential environmental predictors. Multicollinearity among predictors was assessed using variance inflation factors (VIF), with VIF $< 3$ considered acceptable (Zuur et al., 2010). Standard model diagnostics were conducted, including checks for residual normality, homoscedasticity, and multicollinearity. Functional richness showed index-specific responses to combinations of climate, land-use change, current land-use, and soil conditions. We further used variation partitioning *varpart()* function to quantify the independent and shared contributions of climatic, land use, and soil predictors to species and functional richness (Legendre et al., 2012).

All data processing, index calculations, and statistical analyses were performed in R version 4.3.1 (R Core Team, 2023). The following R packages were used: FRic was calculated using the 'FD' package (Laliberté et al., 2014b), while species richness was calculated using 'cati' package (Taudiere and Violle, 2016). Multicollinearity among predictors was assessed using VIF with the *vif()* function from the 'car' package (Zuur et al., 2010). Model selection was performed using the dredge function in 'MuMIn' (Barton, 2023), and multivariate patterns of environmental variables were explored with PCA using 'FactoMineR' and visualised with 'factoextra' (Kassambara and Mundt, 2017). We performed a variation partitioning using the *varpart()* function in the 'vegan' package (Oksanen., 2024). Significance of unique fractions was tested using redundancy analysis *rda()* with permutation ANOVAs. Data manipulation and visualisation were performed using 'dplyr' (Wickham, 2015) and 'ggplot2' (Wickham, 2016).

## 4. Results

At the large-scale (1 km buffer), land-use composition in the Transylvanian wood-pasture systems remained relatively stable over the past six decades (Fig. 2). In the studied sites, forest proportion increased significantly from approximately 35% in 1964 to 45% in 2024 (Appendix S4), and a smaller portion of the forest was replaced by pasture or arable land. Pasture showed only a slightly decreasing extent in 2024 with no significant expansion or contraction (Appendix S4). Arable land experienced the lowest persistence, with several arable patches transitioning into pasture or forest, contributing to a slight

decline in arable area (Appendix S4).

Woody cover at the intermediate-scale (100 m buffer) declined markedly in 21 sites over time. For example, from 92% to 3% or 89% to merely 29%. By contrast, 9 sites showed increases. For instance, from 3% to 28% or from 6% to 25%. These changes are visualised in Fig. 3.

Overall, climatic variables (mean annual temperature and annual precipitation), soil carbon, and land-use variables (current forest cover, current woody cover, pasture change, forest change, and landscape heterogeneity were associated with different responses of species richness, functional richness, and forage quality. Final models explained between 19.2% and 57.5% of the variation in functional richness and forage quality, with the highest $R^2$ for $FRic_{SLA}$ (0.575) and the lowest for $FRic_{SM}$ (0.192). Species richness, $FRic_H$, and forage quality had intermediate $R^2$ values of 0.394, 0.421, and 0.480, respectively (Table 1).

Species richness was positively associated with soil carbon (Fig. 6A) and current woody cover (Fig. 5C), whereas current forest cover showed only a weak positive association. Forage quality was positively associated with annual precipitation (Fig. 4A) but negatively associated with current woody cover (Fig. 5A) and landscape heterogeneity (Fig. 5B). $FRic_H$ was negatively associated with mean annual temperature (Fig. 4B) and pasture loss (Fig. 4C). $FRic_{SLA}$ was positively associated with annual precipitation (Fig. 4D), soil carbon (Fig. 6B), and current forest cover (Fig. 5D), but negatively associated with forest change (Fig. 4E). $FRic_{SM}$ was positively associated only with current forest cover (Fig. 4F).

Variation partitioning showed that climate, current land use, land-use change, and soil conditions jointly contributed to explaining variation in species richness, functional richness, and forage quality, although their relative importance differed among response variables (Table 2). Current land-use variables explained the largest unique proportion of variation in forage quality (adjusted $R^2 = 18.6\%$) and species richness (25.1%), while soil conditions additionally contributed to species richness (13.3%). $FRic_H$ was primarily associated with land-use change (19.5%) and climate (15.2%). $FRic_{SLA}$ showed the highest explained variation overall, with soil conditions accounting for the largest unique fraction (63.9%), followed by current land use (32.1%) and climate (16.1%). In contrast, $FRic_{SM}$ was only weakly explained by the predictor groups, with climate explaining a modest fraction of variation (11.0%) and residual variation remaining high (94.0%).

Proportions of variation uniquely explained by climate, current land use, land-use change, and soil conditions for species richness, functional richness, and forage quality, based on variation partitioning using redundancy analysis (RDA). Values represent adjusted $R^2$ fractions (%). Negative fractions were considered negligible and are presented as 0.

**Table 1**
Summary of model results on the effects of environmental predictors on taxonomic, functional diversity, and forage quality.

| Response | Predictor | Std. Estimate | $R^2$ (%) |
|---|---|---|---|
| Forage quality (QI) | annual precipitation (bio12) | 0.003 * | 48.3 |
| | soil carbon (C) | 0.286 n.s. | |
| | landscape heterogeneity (Shannon index) | −1.568 ** | |
| | current woody cover | −0.018 * | |
| Species richness | soil carbon (C) | 4.248 * | 39.4 |
| | current forest cover | 0.113 n.s. | |
| | current woody cover | 0.276 * | |
| Functional richness of plant height ($FRic_H$) | mean annual temperature (bio1) | −0.152 * | 42.1 |
| | annual precipitation (bio12) | 0.001 n.s. | |
| | pasture change | −0.013 *** | |
| Functional richness of specific leaf area ($FRic_{SLA}$) | annual precipitation (bio12) | 0.002 ** | 57.5 |
| | soil carbon (C) | 0.288 *** | |
| | forest change | −0.009 * | |
| | current forest | 0.007 *** | |
| Functional richness of seed mass ($FRic_{SM}$) | annual precipitation (bio12) | 0.001 n.s. | 19.2 |
| | current forest cover | 0.005 * | |

Significance levels: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, n.s. (not significant)

## 5. Discussion

We studied how multiple environmental factors operating at different spatial scales influence plant taxonomic, functional strategies, and forage quality in traditional wood-pastures in Transylvania, Romania. Our results demonstrate hierarchical environmental filtering in traditional wood-pastures, where climate, woody configuration, and land use jointly but differentially govern plant taxonomic and functional

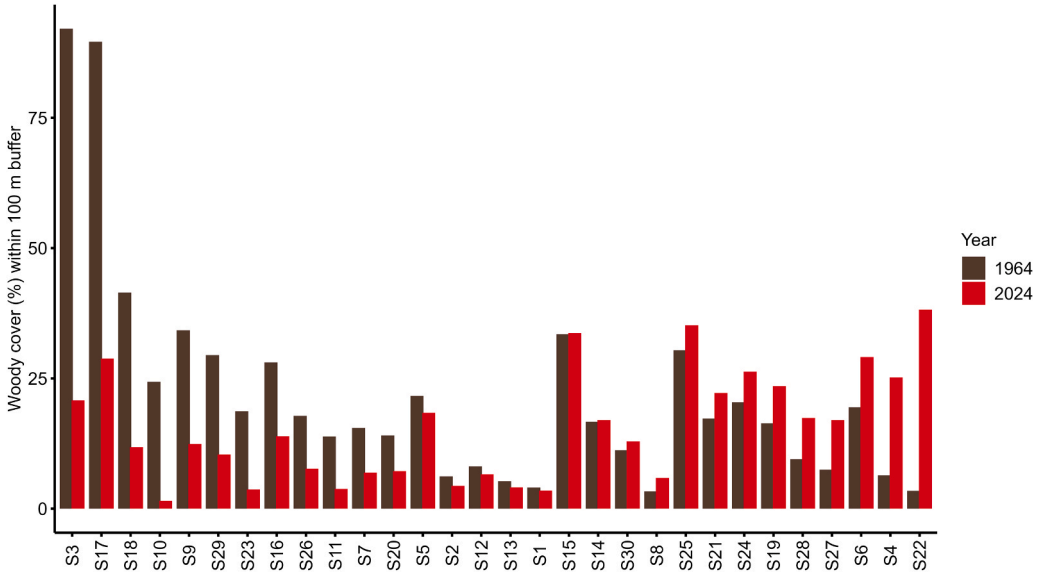


**Fig. 3.** Comparison of woody cover within a 100 m buffer around sampled trees in 1964 and 2024, with sites ordered by the largest change in woody cover between years.

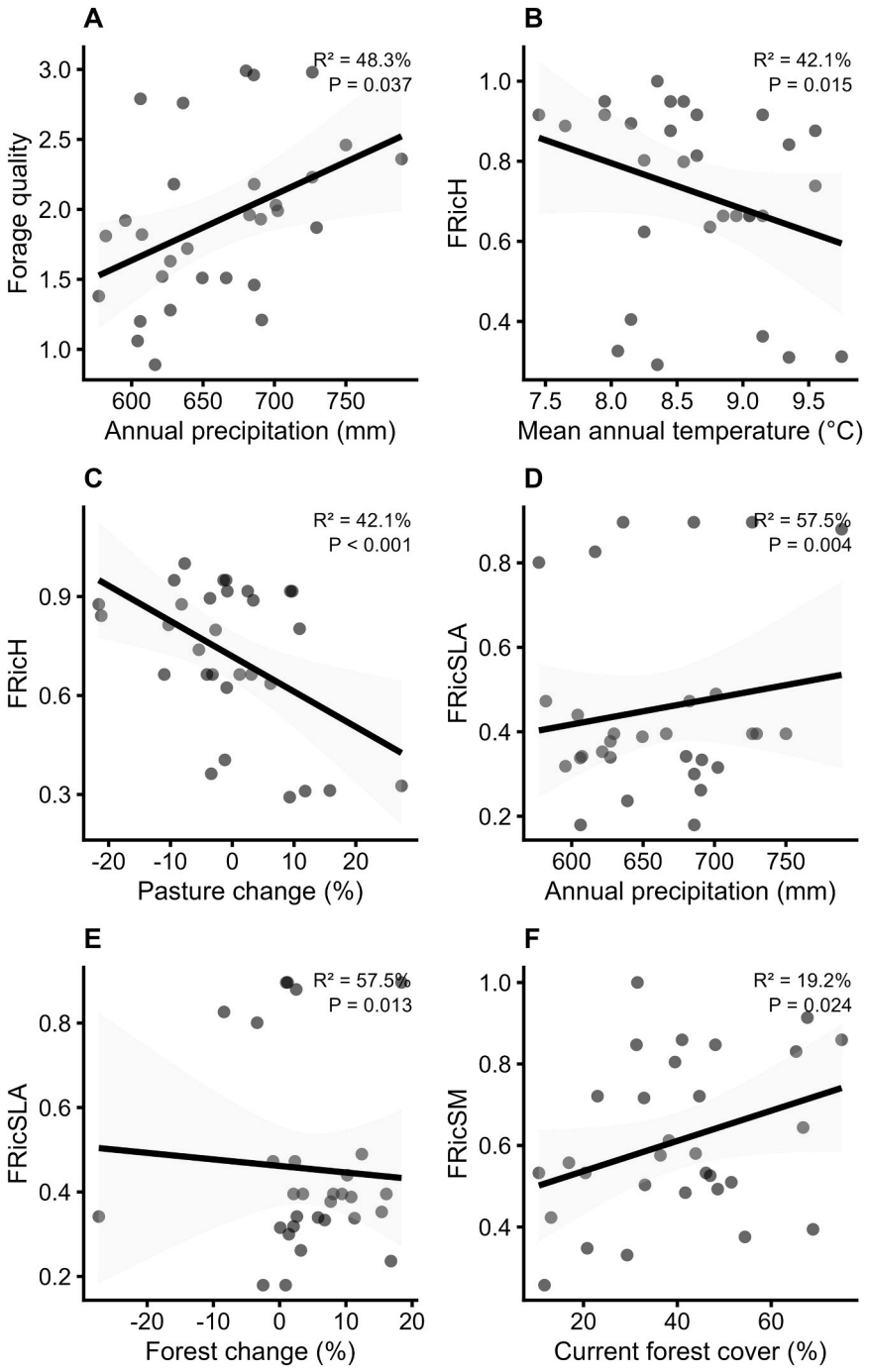


**Fig. 4.** Regression lines showing significant relationships between large-scale environmental predictors and response variables: (A) forage quality (QI) vs. annual precipitation; (B–C) functional richness of plant height ($FRic_H$) vs. mean annual temperature and pasture change; (D–E) functional richness of specific leaf area ($FRic_{SLA}$) vs. annual precipitation and forest change; and (F) functional richness of seed mass ($FRic_{SM}$) vs. current forest cover.

diversity. At the large scale, mean annual temperature was associated with lower $FRic_H$, annual precipitation was linked to higher forage quality and $FRic_{SLA}$, while pasture loss was negatively associated with $FRic_H$ and forest change negatively influenced $FRic_{SLA}$. Current forest cover was linked to higher $FRic_{SM}$ and $FRic_{SLA}$. At the intermediate scale, greater woody cover was associated with higher species richness but lower forage quality, reflecting trade-offs between structural complexity and palatability. At the fine-scale, soil carbon was related to higher $FRic_{SLA}$, and species richness. Overall, plant communities are hierarchically filtered across scales, highlighting the importance of multi-scale drivers for functional diversity and forage quality.

### 5.1. *Landscape stability and land-use composition*

Between 1964 and 2024, Transylvanian traditional wood-pastures showed moderate to high landscape-level stability, with forest expanding mainly over arable land and pasture slightly declining, while woody cover decreased at most sites, indicating local structural rearrangement. This may reflect the long-term influence of low-intensity management and historical land-use continuity (Hartel and Plieninger, 2014; Molnár et al., 2015). Only a slight increase in forest cover accompanied a decline in arable land, in line with previous findings (Munteanu et al., 2014; Petrişor and Petrişor, 2017). This persistent mosaic of open grasslands,

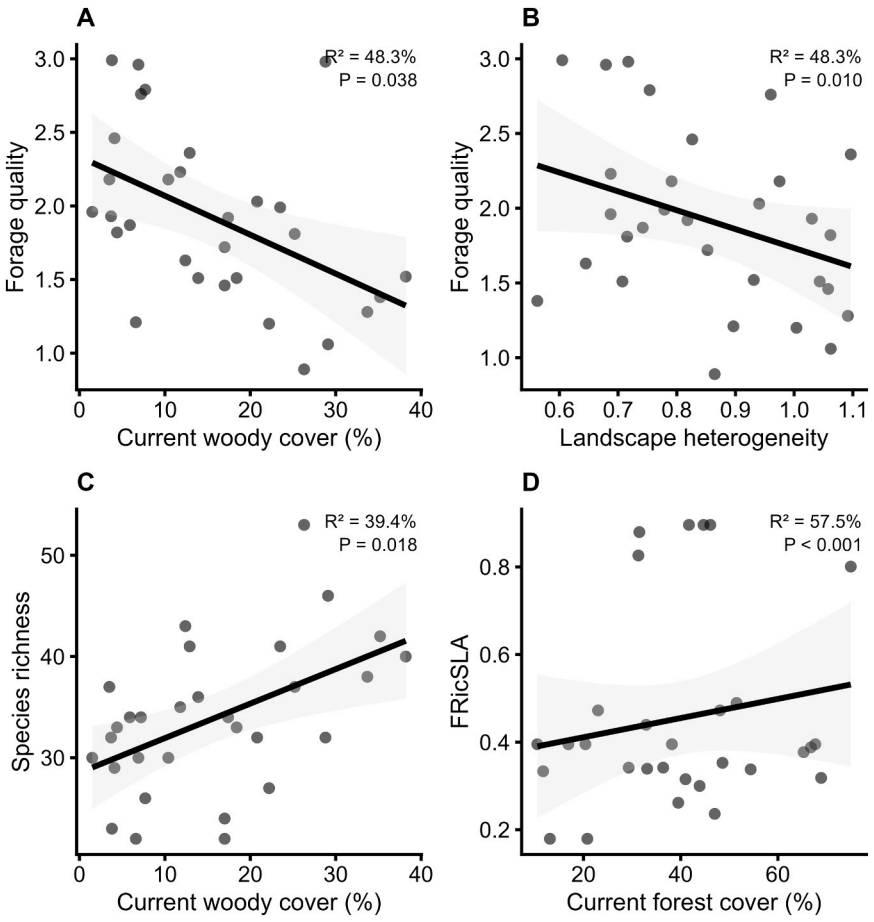


**Fig. 5.** Regression lines showing significant relationships between intermediate-scale vegetation structure and response variables: (A–B) forage quality (QI) vs. current woody cover and landscape heterogeneity (Shannon index); (C) species richness vs. current woody cover; and (D) functional richness of specific leaf area ($FRic_{SLA}$) vs. current forest cover.

scattered trees, and forest edges, which supports high ecological and cultural value, resembles other traditionally managed European wood-pastures (Plieninger et al., 2003; Manning et al., 2006). Compared with many Western and Central European regions, where intensification or abandonment has rapidly homogenised landscapes (Chamberlain and Siriwardena., 2000), Transylvanian systems have largely retained landscape-scale heterogeneity despite socio-economic change.

At the same time, the decline in pasture area and increase in forest cover indicate land abandonment and natural succession that have affected many Eastern European agro-pastoral landscapes (Hartel et al., 2013; Munteanu et al., 2014; Plieninger et al., 2015). These changes are associated with a reduction in open pasture habitat and increasing woody encroachment, favouring competitively dominant and shade-tolerant taxa over short-statured, disturbance-tolerant, and

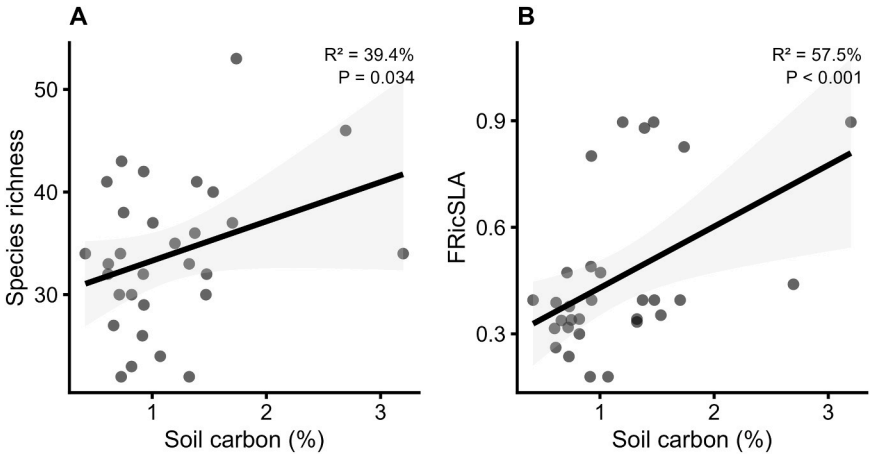


**Fig. 6.** Regression lines showing significant relationships between fine-scale soil conditions and response variables: (A) species richness vs. soil carbon; and (B) functional richness of specific leaf area ($FRic_{SLA}$) vs. soil carbon.

**Table 2**
Variation partitioning based on RDA of species richness, functional richness, and forage quality, explained by climate, current land use, land-use change, and soil conditions.

| Response | Climate (%) | Current land use (%) | Land-use change (%) | Soil (%) | Residual | $R^2$ (%) |
|---|---|---|---|---|---|---|
| Forage quality (QI) | 0.0 | 18.6 | 0.0 | 6.9 | 65.3 | 34.7 |
| Species richness | 0.0 | 25.1 | 10.4 | 13.3 | 65.8 | 34.2 |
| Functional richness of plant height ($FRic_H$) | 15.2 | 1.1 | 19.5 | 0.0 | 71.7 | 28.3 |
| Functional richness of specific leaf area ($FRic_{SLA}$) | 16.1 | 32.1 | 6.0 | 63.9 | 53.5 | 46.5 |
| Functional richness of seed mass ($FRic_{SM}$) | 11.0 | 4.1 | 2.3 | 0.0 | 94.0 | 6.0 |

light-demanding species(Öllerer., 2014; Török et al., 2018). Pasture loss, therefore, represents not only a change in land-cover class but a functional shift in vegetation assembly processes.

Moreover, apparent land-cover stability concealed important fine-scale structural changes. Woody cover declined at most sites, even where overall land-cover classes remained stable, indicating structural degradation (Lindenmayer, 2017; Fischer et al., 2012). This decline likely reflects interacting processes, including selective harvesting, removal of trees to maintain grazing areas, and insufficient regeneration of senescent individuals (Manning et al., 2006; Hartel et al., 2013; Oldén et al., 2017). Changes in grazing regimes may further constrain regeneration through browsing pressure or, locally, promote recruitment where grazing declines (Allred et al., 2012; Wadud et al., 2024). Together, these processes gradually undermine habitat heterogeneity, microclimatic buffering, and regeneration potential.

### 5.2. Multi-scale drivers of plant diversity and forage quality

At the large-scale, higher annual precipitation was associated with higher forage quality and $FRic_{SLA}$, suggesting that wetter conditions support a broader range of acquisitive plant strategies and more productive vegetation. In contrast, mean annual temperature was negatively associated with $FRic_H$, indicating that warmer conditions may favour a narrower range of plant strategies, in line with environmental filtering (Freschet et al., 2011; Gross et al., 2013; Nunes et al., 2017). These patterns are consistent with environmental filtering theory, which predicts that increasingly stressful conditions select for functionally similar species, whereas more productive environments relax these constraints and promote greater functional differentiation among species (Weiher and Keddy, 1995). Regarding land-use change, a decline in pasture extent over time was linked to lower $FRic_H$, indicating a narrowing of the range of plant stature in these communities. As such, this pattern is related to habitat filtering since the increase in extention of one habitat filter species is adapted to those habitat conditions. This pattern likely reflects habitat filtering, whereby the expansion of a single habitat type may favour species adapted to those specific environmental conditions (Puglielli et al., 2024). In contrast, a decrease in the dominance of pasture at the landscape level, and the presence of a mosaic of habitats, may facilitate the coexistence of functionally distinct species, each of them adapted to specific and diverse habitat conditions. Similarly, forest change over time was negatively associated with $FRic_{SLA}$, suggesting that long-term shifts in forest cover may link to constrain variability in leaf economic strategies (Carmona et al., 2012; de Bello et al., 2013; Török et al., 2018). Current forest cover was positively associated with $FRic_{SM}$ and $FRic_{SLA}$, indicating a broader range of trait values in more forested areas. These apparently opposite findings compared to the increase of arable and forest over time, are in line with literature since in wood-pastures, largely dominated by open habitats, the increase of forest cover favours the presence of species adapted to shadow-conditions (Le et al., 2025b). This illustrates that a moderate increase in forest in this system modifies plant communities not only in terms of increasing functional diversity, but also increasing species richness (Eldridge et al., 2011; Bernardi et al., 2016; Erdős et al., 2024; Le et al., 2025b).

At the intermediate-scale, woody cover was positively linked to species richness but negatively associated with forage quality, reflecting a trade-off between structural complexity and palatability. Canopy structure modifies light availability, microclimate, and litter deposition, thereby influencing competitive hierarchy and trait distribution (Manning et al., 2006; Eldridge et al., 2011; Carmona et al., 2012). Canopy and tree structure from current forest cover was positively associated with $FRic_{SLA}$, suggesting that structurally heterogeneous landscapes generate environmental gradients in light, litter, and moisture that facilitate the coexistence of fast-growing, acquisitive species and slower, more conservative species, consistent with findings in Mediterranean dehesas and montados (Carmona et al., 2012; Erdős et al., 2024).

At the fine-scale, soil carbon was related to higher species richness and $FRic_{SLA}$, reflecting nutrients-mediated coexistence and competitive sorting among species with contrasting resource strategies (Cornelissen et al., 2003; Laliberté et al., 2014a). Higher soil carbon likely increases local resource availability and improves soil moisture retention, thereby creating more favourable microsite conditions that support the coexistence of a broader range of plant species and functional strategies (Perring et al., 2016; De Long et al., 2023). Soil carbon influenced local trait expression and dominance hierarchies rather than driving broad-scale species turnover, highlighting its role in fine-scale functional filtering (Bugalho et al., 2011; De Long et al., 2023). Our findings are in line with previous studies that local scale, such as woody cover and soil, have a stronger impact on plant functional diversity than at the landscape scale (Mugnai et al., 2022).

### 5.3. Relative contributions of spatial scales to plant diversity and forage quality

Variation partitioning showed that climate, current land use, land-use change, and soil conditions contributed differently to the observed biodiversity patterns. Current land-use variables explained the largest unique proportion of variation in forage quality and species richness, highlighting the importance of woody structure and landscape configuration for local community composition (Manning et al., 2006; Eldridge et al., 2011). In contrast, $FRic_H$ was more strongly associated with climate and land-use change, particularly pasture loss. This is consistent with studies showing that grazing abandonment and climatic filtering influence plant stature and competitive strategies (Pakeman, 2011; Török et al., 2018). $FRic_{SLA}$ showed the highest explained variation overall and was primarily associated with soil conditions, followed by current land use and climate, suggesting strong fine-scale environmental filtering of leaf economic strategies (Cornelissen et al., 2003; Laliberté et al., 2014a). $FRic_{SM}$ showed comparatively weak explanatory power, indicating that additional local processes, such as dispersal limitation, grazing intensity, or microsite heterogeneity, may play a stronger role in shaping seed-mass variation (Westoby et al., 1998; de Bello et al., 2013). Overall, these findings support hierarchical filtering, showing that different biodiversity facets respond to distinct combinations of environmental constraints and land-use dynamics (de Bello et al., 2010; Laliberté and Legendre, 2010).

### 5.4. Trade-offs between woody cover and forage quality

Woody cover creates a fundamental structural trade-off that shapes forage quality in wood-pasture systems (Nelson and Moser, 1994; de Jalón et al., 2018; Ripamonti et al., 2025). High woody cover is generally associated with reduced light and soil resource availability, limiting fast-growing, nutrient-rich species and favouring shade-tolerant, slow-growing species with lower forage quality (Jackson and Ash, 1998). By contrast, low woody cover is associated with productive, nutrient-rich and light-demanding grasses but reduces structural heterogeneity (Tölgyesi et al., 2023). As a result, intermediate and spatially heterogeneous woody cover is most likely to balance biodiversity conservation with forage provisioning (Manning et al., 2006; Crous–Duran et al., 2019; Kachler et al., 2023). Additionally, grazing may further modulate these structural trade-offs by influencing biomass accumulation, woody recruitment, and species competition (Schmucki et al., 2012; Zheng et al., 2015; Cao et al., 2024). Maintaining moderate grazing helps preserve open conditions and promotes palatable, disturbance-adapted species, thereby enhancing forage quality. By contrast, grazing abandonment can lead to canopy closure and litter accumulation, while overgrazing reduces plant diversity and soil functioning, ultimately compromising forage quality (Oldén et al., 2017). Therefore, sustaining multifunctional wood-pastures requires adaptive, low-intensity grazing regimes that balance herbaceous productivity, tree regeneration, and overall ecosystem resilience.

Our study has limitations that should be acknowledged. First, functional diversity metrics were calculated using species-level trait values obtained from global trait databases and therefore did not account for intraspecific trait variation under local environmental conditions (Violle et al., 2012; Bricca et al., 2026). However, intraspecific trait variability has a smaller magnitude compared to between- species trait variation (Jung et al., 2010), supporting the robustness of our species- level approach (e.g., de Bello et al., 2013; Kambach et al., 2023). Second, environmental predictors were quantified across multiple spatial scales, whereas plant diversity was assessed only at the local scale using the local species pool derived from three merged 1 m × 1 m vegetation plots around each sampled tree. Consequently, the identified relationships reflect drivers of local-scale taxonomic and functional diversity and may differ at broader spatial scales (Chase and Knight, 2013). Third, additional factors not included in the analyses, such as grazing intensity, local management history, or microsite heterogeneity, may also contribute to the observed patterns (Pakeman, 2011; Török et al., 2018).

## 6. Conclusions

Plant communities in Transylvanian wood-pastures reflect the combined influence across multiple scales of climate, past management, vegetation structure, and soil conditions. Mean annual temperature, precipitation, and pasture and forest change were associated with shifts in functional composition, while current forest cover and woody cover were associated with species richness, forage quality, and functional richness related to leaf economics and seed mass. Fine–scale variation in soil properties further supports the coexistence of divergent strategies, sustaining functional diversity and forage quality. These findings highlight that maintaining hierarchical ecological processes: from landscape–level climate and land-use legacies to local structural and soil heterogeneity, is essential for conserving biodiversity, supporting ecosystem function, and guiding sustainable management and restoration of traditional wood-pastures.

These insights further indicate that conserving wood-pastures requires more than preserving their visible landscape mosaic. Functional changes can occur even in seemingly stable landscapes, underscoring the need to consider management history when designing interventions. Maintaining moderate grazing, preventing shrub encroachment, and safeguarding scattered trees and forest edges remain crucial for sustaining functional diversity. Monitoring soil conditions may help detect subtle shifts in dominance patterns.

Our study area in Romania shows a large potential for nature conservation as well as ecosystem and landscape restoration with regard to the diversity of traditional land-use types and practices. Particularly with regard to traditionally managed wood-pastures and forests. However, biodiversity and ecosystem services' provision have to be well-balanced in conservation and restoration programs. Priority on carbon sequestration and accumulation, as well as typical forest species (e.g., with high seed mass and sensitivity to disturbances), could give guidance for an increase in forest area. Species diversity, with plant (and animal) species particularly characteristic of open land and rare and threatened species, could favour the restoration of traditional wood-pastures.

## CRediT authorship contribution statement

**Thuy Hang Le:** Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Alessandro Bricca:** Writing – review & editing, Visualization, Formal analysis, Conceptualization. **Stefan Zerbe:** Writing – review & editing, Supervision, Project administration, Funding acquisition. **Adrian Indreica:** Writing – review & editing, Visualization, Methodology, Formal analysis, Data curation, Conceptualization. **Johannes Metz:** Writing – review & editing. **Sachin Bhattarai:** Data curation. **Martin Sauerwein:** Project administration, Funding acquisition. **Gianmaria Bonari:** Writing – review & editing, Supervision, Methodology, Conceptualization.

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## Supplementary materials

Supplementary material associated with this article can be found in the online version.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2026.110716.

## Data Availability

Data will be made available on request.

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