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Herb layer vegetation patterns of silvopastoral systems: the interactive role of succession, disturbance and seed bank

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Abstract Due to their heterogeneous landscape structure, extensively managed temperate silvopastoral systems provide multiple ecosystem services such as climate-resilient livestock production and carbon sequestration. Main habitat types within these landscapes (open pastures, solitary trees, shrubby patches, and adjacent second-growth forests) form an interconnected dynamic network with state transitions driven by secondary succession (towards woody states) and disturbance (towards open states), and the balance between the drivers is key to preserve their exceptionally rich herbaceous flora. To understand how soil seed bank may contribute to the dynamics of the herb layer in silvopastoral systems, we assessed its composition and richness in the above-mentioned habitats and compared these to the herb layer using non-metric multidimensional scaling, generalized linear mixed-effects models and indicator species analyses. We found that each habitat showed distinct compositional patterns, explained by strong

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environmental filters. Conversely, soil seed bank was more similar among habitats due to legacy seeds from previous vegetation states. This ecological memory in a particular location may assist future compositional transitions of the herb layer by reducing dispersal limitation and can be a useful asset in ecosystem restoration. Furthermore, our study showed that solitary trees with grassy or shrubby undergrowth have key roles in the herb layer dynamics of silvopastoral systems by being the main locations of soil seed bank build-up and transitional hotspots of herb layer diversity during early forest succession. Therefore, conservation strategies should pay extra attention to these small but important landscape features.

Keywords Traditional land-use · Scattered trees · Shrub encroachment · State transition · Grazing · Wood-pasture

Introduction

Traditional silvopastoral systems belong to the most ancient land-use types in Europe, known since the Neolithic era (Bergmeier et al. 2010; Roellig et al. 2018), and are also present in the Americas (Peri et al., 2016; Orefice et al. 2017), Asia (Liu et al. 2024) and Australia (Bird et al. 2010). Most silvopastoral systems were created in former forest landscapes by partial clearing and subsequent grazing and pastureland management, to form an open landscape with solitary trees scattered in an open pasture matrix (Bergmeier et al. 2010; Varga & Molnár 2014; Plieninger et al. 2015; Roellig et al. 2018), mimicking landscapes once sustained by megaherbivores that went extinct long ago (Erdős et al. 2022).

Scattered trees are considered keystone structures of silvopastoral systems because of their large ecological role in maintaining biodiversity and providing a broad range of ecosystem services (e.g. fruit and shade for livestock), relative to their small spatial extent (Manning et al. 2006; Lindenmayer 2017; Torralba et al. 2018). As trees alter the microclimate and soil properties under their canopies, they create microhabitats for a wide range of organisms otherwise not found in open grasslands (López-Sánchez et al. 2016; Lőrincz et al. 2024), such as forest-specific saproxylic beetles and flies (Falk 2014), woodland birds (Hartel et al. 2014) and forest specialist plants (Tölgyesi et al., 2018). Despite their long history of traditional management and multifunctionality, ancient silvopastoral systems are declining rapidly in Europe (Roellig et al. 2018; Pereponova and Skaloš, 2019) due to i) shrub encroachment and forest regrowth caused by land abandonment, or ii) decreasing tree cover caused by reduced tree recruitment (Bergmeier et al. 2010; Bergmeier and Rolling, 2014; Hartel et al. 2018). Both of these trends compromise the vegetation dynamics of silvopastoral systems, characterised by a balance between secondary succession (expansion of woody species) and disturbance (livestock grazing), leading to a loss of habitat heterogeneity and overall biodiversity (Tölgyesi et al., 2018; Simonson et al. 2018).

Although shrub encroachment is typically associated with reduced pastoral productivity in many grazed semi-natural grasslands (Eldridge et al. 2011; Ding and Eldridge 2024), recent studies have shown that a certain amount of shrubby patches is crucial for ensuring the vegetation dynamics of silvopastoral systems, because shrubs can facilitate the regeneration of trees by serving as nurse plants (Rivest et al. 2011; Rolo et al. 2013; Oksuz et al. 2020). Despite their small patch size, shrubs can increase the plant species richness in these landscapes as they support distinct vegetation with greater diversity of shade-tolerant forest species (Eldridge et al. 2011; Teleki et al., 2020; Oksuz et al. 2020). In the long run, this distinct vegetation type gradually gains a structure and species composition that is more similar to that of nearby forest than to open grassland, indicating that these patches represent an intermediate state in the grassland-forest transition (Ratajczak et al., 2017; Tölgyesi et al., 2018). These new forest patches adjacent to grazed parts of the silvopastoral systems are often used as coppice-wood (Falk 2014; Garbarino and Bergmeier 2014) and can be reverted to an open state after cutting, if needed.

To keep up with the recruitment of woody plants, forest-specific herbaceous species may use two ways for colonisation: active dispersal from the closest forest patch or emerging from soil seed banks. Seed bank composition depends on the present and previous aboveground vegetation, on the seed rain from the surrounding areas, and on the

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longevity of the seeds (Bekker et al. 1998; López-Mariño et al., 2000; Baskin and Baskin 2014). On ecological and evolutionary timescales, soil seed banks represent local ‘biodiversity reservoirs’ that can play an important role in population dynamics, in determining the composition and structure of future plant communities, and in maintaining the genetic and functional trait diversity of local populations (Bakker et al. 1996a; Bossuyt and Honnay 2008; Faist et al. 2013; Vandvik et al. 2016). Moreover, seed banks play a crucial role in the spontaneous recovery and restoration potential of plant communities of conservation importance (Bakker et al. 1996b; Bossuyt et al. 2002; Faist et al. 2013; Ludewig et al. 2021), as they might contain seeds of the target species even after the species disappeared from the aboveground vegetation (Hopfensperger 2007; Kalamees et al. 2012; Shiferaw et al. 2018). Producing seeds that remain viable in the soil for a certain period of time allows plant species to bridge temporarily unsuitable habitat conditions (Bossuyt and Honnay 2008), thus soil seed banks might reflect ‘ecological memories’ of past ecosystem conditions (Bakker et al. 1996b; Vandvik et al. 2016), which can be a useful feature in landscapes with cyclic dynamics, such as silvopastoral systems. Seed banks can also provide considerable resilience against disturbance or environmental change (Johnstone et al. 2016; Ma et al. 2021), since their composition generally changes slower than that of the aboveground vegetation. Therefore, if the seed bank still reflects the desired state (pre-disturbance composition of the aboveground vegetation), the system has some potential to retain resilience (Ma et al. 2021).

However, the relationship between seed bank and aboveground herb layer vegetation patterns and dynamics has received little attention in silvopastoral systems (but see e.g. Franca et al. 2018). To improve our understanding in this respect, we studied them in three temperate silvopastoral systems in Romania and hypothesised that (i) the aboveground herb layer vegetation of different landscape features (open pastures, solitary trees, shrub-encroached patches and second-growth forests) is rather distinct, but (ii) due to the cyclic vegetation dynamics, their seed banks are more similar and thus can support compositional transitions in either direction. Consequently, seed banks may provide some resilience to external impacts threatening the rich herb layer flora of silvopastoral systems.

Materials and methods

Study site

The study was carried out in three Romanian silvopastoral systems, near the villages of Deuşu (N46.916, E23.505), Mercheasa (N46.058, E25.368) and Ticuşu Vechi (N45.909, E25.134) (Fig. 1A). Altitudes range from 420 to 660 m. The climate is continental with a mean annual temperature of 8.0 – 8.3 °C and a mean annual precipitation of 600 – 650 mm (Hartel et al. 2013; 2018). The landscape is hilly with gentle slopes. The area of the silvopastoral systems is 246 ha (Deusu), 825 ha (Mercheasa) and 800 ha (Ticuşu Vechi), and are surrounded by treeless, more intensive pastures and closed-canopy oak-hornbeam forests. These forests represent the potential natural vegetation of the region (in the absence of the ancient wild megaherbivore fauna), although most of them are second-growth and were more open and used for grazing for some periods in the past centuries. The density of old scattered trees is 0.5–1 ha^{-1}, and most of them are oaks (*Quercus petraea* and *Q. cerris*), but a few wild pears (*Pyrus pyraster*) and hornbeams (*Carpinus betulus*) also occur. All silvopastoral systems are grazed by sheep all year round, which is complemented with cattle and buffalo grazing (and with horse in Mercheasa) during the growing season (Hartel et al. 2018; Tölgyesi et al. 2023). The effects of grazing livestock (e.g., trampling and manure) are more concentrated under scattered trees than in open pastures as animals frequently find shelter under their canopies from the heat of the sun. However, trees that are not visited by livestock for some time can quickly develop a thorny shrubby undergrowth (e.g., with *Crataegus monogyna* and *Prunus spinosa*). As these areas become less accessible for grazing and serve as hiding places for large predators, like brown bears (*Ursus arctos*), they are avoided by the livestock, allowing natural succession to progress towards a forest state. Shrub encroachment in grazed open parts is rare.

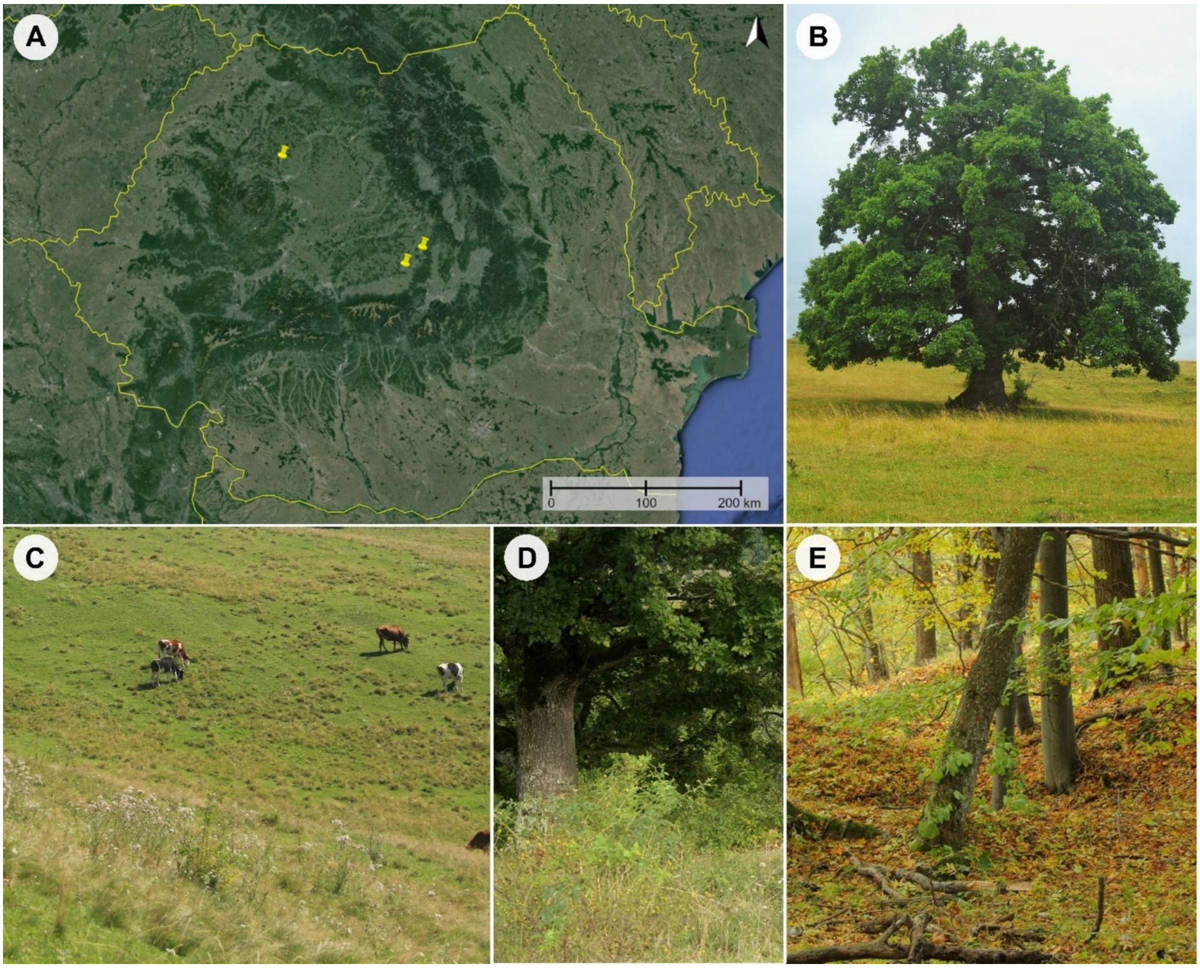


Fig. 1 Location of the three studied silvopastoral systems in Romania, Eastern Europe **A**, and the four studied habitat types: trees with grass **B**, open pastures **C**, trees with shrubs **D**, and second-growth forests **E**

Site selection

We studied four habitat types: open pastures (i.e. the grassy parts of the silvopastoral systems; Fig. 1C), scattered trees with grassy undergrowth (hereafter "trees with grass"; Fig. 1B), scattered trees with shrub-encroached undergrowth (hereafter "trees with shrubs"; Fig. 1D), and adjacent second-growth oak-hornbeam forests (hereafter "forests"; Fig. 1E). We selected eight sites in each habitat type in each silvopastoral system, thus we had 32 sites per locality and 96 sites in total. The distance between sites was at least 100 m to ensure spatial independence. For scattered trees, we chose mature oak trees with a diameter at breast height between 70–100 cm. Sites in open pastures were situated at least 30 m from the edge of the closest tree canopy. Sites in forests were placed at least 100 m from the forest edge.

Herb layer vegetation

We established three 1 m × 1 m plots in each site both in spring and in summer, 2020 (576 plots in total). Plots under tree canopies were placed 2–3 m from the tree trunk. In each plot, we visually estimated the percentage cover of all vascular plant species in the herb layer. We included woody vegetation (tree saplings and shrubs) only if their height was below 50 cm. We averaged the plot triplets of each site into a site sample and data of spring and summer samplings were merged into one dataset (96 vegetation records in total). If a species had both spring and summer cover values, we used the larger value for subsequent data analyses.

Seed bank

We analysed the soil seed bank with the seedling emergence method. We collected five replicates of soil cores (depth: 10 cm, diameter: 4 cm, volume: 126 cm^3) from each site after snowmelt in 2020 (480 soil cores in total). We pooled and treated cores from the same site together during sample processing (96 soil samples in total). Following the standard methodology of ter Heerdt et al. (1996), we concentrated soil samples by sieving. First, we separated large organic and inorganic particles (e.g., root fragments or gravel but not large seeds) by washing over a coarse sieve (mesh size: 4 mm), then we washed out the fine soil grains using a sieve with 0.2 mm mesh size, which is well below the lower size limit of most seeds. We spread the concentrated soil samples in a 3–4 mm thick layer on trays filled with steam-sterilised potting soil and placed them under natural light in a greenhouse located in the Botanical Garden of the University of Debrecen. We regularly checked, counted, and, if possible, identified the emerging seedlings to species level. Unidentified seedlings were transplanted and grown until their identification was possible. We watered the pots regularly from April until early July, when no seedlings emerged. We resumed watering only in late August and continued until the end of October. We used sample-free control trays, which were filled with steam-sterilised potting soil as control and monitored accidental seed contamination in them.

Data analysis

To visualise the compositional patterns of habitat types, we applied non-metric multidimensional scaling (NMDS) with Raup-Crick dissimilarity (a metric based on presence-absence data) for the herb layer vegetation and the soil seed bank, separately, following Plue et al. (2021). In the case of the seed bank, we excluded two outlier forest records from the NMDS as they both contained a single species otherwise not found in the other records (*Carpinus betulus*, i.e. a tree species, which is of little importance in our herb layer focused study). To test the effect of habitat type (open pastures, trees with grass, trees with shrubs, and forests) on the composition of the herb layer vegetation and seed bank, we calculated pairwise permutational multivariate analysis of variance (PERMANOVA) among habitat types, separately for the herb layer vegetation and the seed bank, based on Raup-Crick dissimilarity and 999 permutations. The *p*-values were adjusted for multiple comparisons with the FDR method.

In order to better quantify between-habitat heterogeneity of the herb layer vegetation and seed banks, we calculated distance matrices between pairs of habitat types (six possible pairs combined from the four habitats), using Raup-Crick dissimilarity. After this, we tested the effects of the data type (herb layer vegetation or seed bank) on the distances for each habitat pair with linear mixed-effects models (LMMs). In the models, distance was used as the response variable, data type was included as the fixed factor, while locality (either of the three silvopastoral systems) was included as a random factor.

To identify species that are strongly associated with one of the habitat types (i.e. are important contributors to between-habitat compositional heterogeneity), we performed indicator species analyses on the herb layer vegetation and seed bank data, separately, using log-transformed abundance data. Significance level was set to $p = 0.01$ (cf. Erdős et al. 2018).

We grouped all species found in the herb layer vegetation and seed bank according to their habitat preferences to grassland, forest and ruderal communities using Sârbu et al. (2013) (Tables S1 and S2). We aimed to use the balance between grassland and forest species to understand the dynamics between grassland and forest states in the silvopastoral systems, while we also aimed to understand the level of accompanying disturbance regimes by also considering ruderal species. For this, we tested the effects of habitat type on the species richness in the three species groups (grassland, forest, and ruderal species) in the herb layer vegetation and in the seed bank using generalized linear mixed-effects models (GLMMs) with Poisson error distribution. Species richness was included as response variable, habitat type (open pastures, trees with grass, trees with shrubs, and forests) as the fixed factor, and locality as a random factor. We excluded tree species from the analyses of forest species as trees do not have a preference for forest communities; rather they make them forest communities.

We performed all analyses in R v. 4.2.2 (R Core Team 2022). We used the *metaMDS* and the *adonis2* functions of the ‘vegan’ package for NMDS ordinations and for pairwise PERMANOVAs, respectively (Oksanen et al. 2018). For calculating the distance matrices, we used the *vegdist* function of the ‘vegan’ package (Legendre and Legendre 2012). For identifying indicator species, we applied the *multipatt* function of the ‘indicspecies’ package (De Caceres et al. 2010), using 999 permutations. For LMMs and GLMMs, we used the *lmer* and *glmer* functions, respectively, of the ‘lme4’ package (Bates et al. 2015), the *Anova* function of the ‘car’ package to test model significances (Fox and Weisberg 2019), and the *emmeans* function of the ‘emmeans’ package to calculate pairwise comparisons (Lenth 2021).

Results

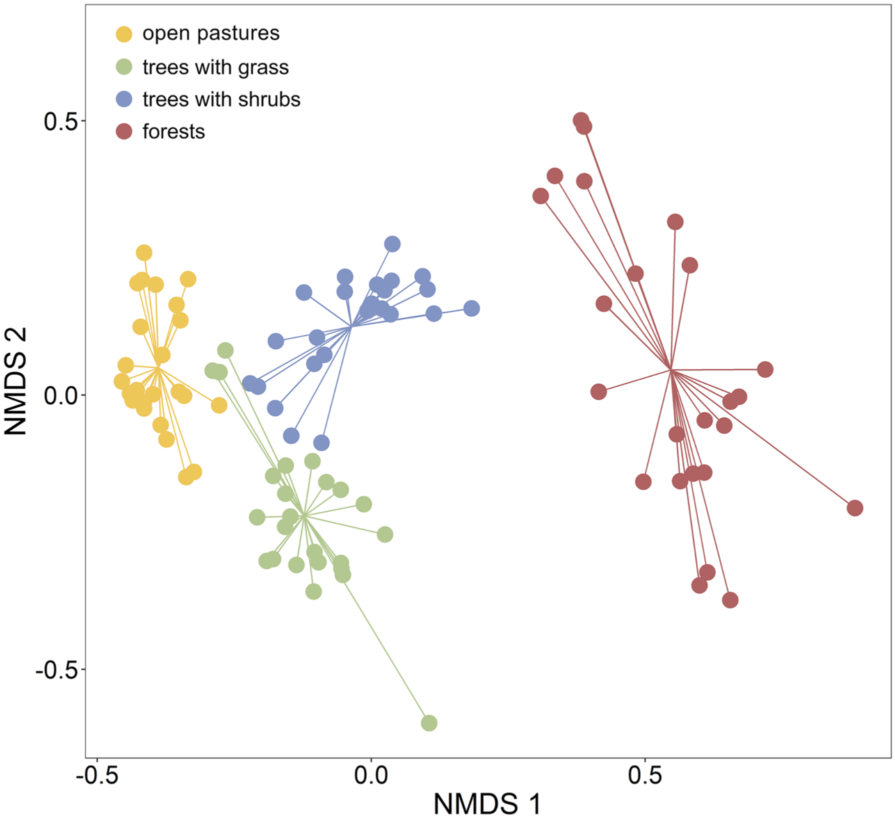
Species composition

According to the NMDS ordination of the vegetation records (stress factor: 0.09), the herb layer of each habitat type occupied rather distinct regions in the ordination space (Fig. 2). Forest plots scattered far from the other three habitat types in the ordination space. Trees with grass and trees with shrubs were between the open pasture and forest states but did not align along a straight trajectory between them.

The NMDS ordination of the seed bank records (stress factor: 0.20) showed a slight distinction among the four habitat types in the ordination space (Fig. 3).

According to the pairwise PERMANOVAs, compositional differences both in the herb layer vegetation and in the seed bank among habitat types were significant, although in the seed bank the difference between trees with grass and forests were only marginally significant (Table 1). However, the R^2 values

Fig. 2 NMDS ordination of the herb layer vegetation of the four habitat types from the three studied silvopastoral systems in Romania, using Raup-Crick dissimilarity



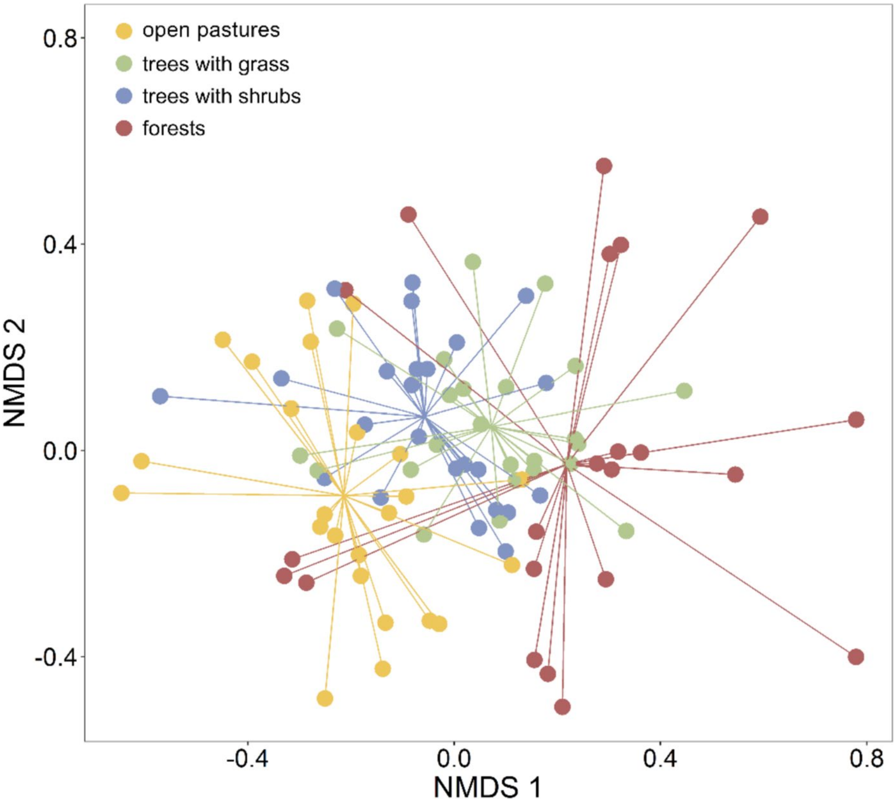


Fig. 3 NMDS ordination of the seed banks of the four habitat types from the three studied silvopastoral systems in Romania, using Raup-Crick dissimilarity

Table 1 Pairwise comparisons of the species composition of the herb layer vegetation and of the seed bank among the four habitat types (OP: open pastures, TG: trees with grass, TS: trees with shrubs, and FO: forests) with pairwise permutational multivariate analysis of variance (PERMANOVA). The *p*-values were adjusted with the FDR method. Significant differences ($p < 0.05$) are marked with boldface

Habitat type	Herb layer vegetation			Seed bank		
	R^2	F	*p*	R^2	F	*p*
OP – TG	0.96	1013.9	**< 0.001**	0.50	45.49	**0.003**
OP – TS	0.97	1793	**< 0.001**	0.19	10.73	**0.008**
OP – FO	0.87	317.64	**< 0.001**	0.24	14.41	**0.003**
TG – TS	0.95	796.35	**< 0.001**	0.24	14.55	**0.008**
TG – FO	0.78	161.14	**< 0.001**	0.07	3.29	0.088
TS – FO	0.64	83.51	**< 0.001**	0.11	5.46	**0.019**

were always two to three times higher in the herb layer vegetation than in the seed bank.

Between-habitat heterogeneity

According to the LMMs, the compositional differences between habitat type pairs were always significantly smaller in the seed bank than in the herb layer vegetation (Table 2).

Indicator species

The herb layer vegetation of open pastures harboured 14 indicator species (9.2% of all species recorded in the herb layer of open pastures) (Table 3). These

Table 2 Test results of the linear mixed-effects models (LMMs) used for calculating the similarity of the habitat types in the herb layer vegetation and the seed bank between pairs of habitat types (OP: open pastures, TG: trees with grass, TS: trees with shrubs, and FO: forests). Significant differences ($p < 0.05$) are marked with boldface

	vegetation mean ± sd	seed bank mean ± sd	F	p
OP – TG	0.05 ± 0.16	0.27 ± 0.29	88.17	**< 0.001**
OP – TS	0.03 ± 0.07	0.22 ± 0.23	123.27	**< 0.001**
OP – FO	0.96 ± 0.09	0.49 ± 0.38	282.07	**< 0.001**
TG – TS	0.07 ± 0.17	0.18 ± 0.25	28.33	**< 0.001**
TG – FO	0.62 ± 0.29	0.42 ± 0.35	38.84	**< 0.001**
TS – FO	0.42 ± 0.33	0.41 ± 0.37	0.121	0.728

species were mostly grazing-tolerant legumes (e.g., *Lotus corniculatus*), short grasses (e.g., *Festuca pseudovina/rupicola* and *Anthoxanthum odoratum*) and rosette-forming dicots (e.g., *Hypochaeris radicata*) typical of pastures. Trees with grass had eight indicator species (5.9% of all species recorded in the herb layer of trees with grass). All of them were ruderal, disturbance-tolerant species (e.g., *Poa annua*). Trees with shrubs harboured 34 indicator species (13.4% of all species recorded in the herb layer of trees with shrubs). These species belonged to a variety of species groups, like spiny shrubs (e.g., *Crataegus monogyna* and *Rosa canina* agg.), tree seedlings (e.g., *Quercus petraea*), forest herbs (e.g., *Clinopodium vulgare*), short, grazing-tolerant species (e.g., *Fragaria vesca*), taller, grazing-sensitive species (e.g., *Hypericum perforatum*) as well as ruderal species (e.g., *Cirsium vulgare*). Forests had 11 indicator species (9.8% of all species recorded in the herb layer of forests), consisting of only oak-hornbeam forest species (e.g., *Anemone nemorosa* and *Sanicula europaea*).

The analysis of indicator species of the soil seed bank records revealed that the seed banks in all habitat types had less indicator species than the herb layer vegetation (Table 2). Open pastures had only two indicator species (2.6% of all species recorded in the seed bank of open pastures): *Plantago lanceolata*, a grazing-tolerant forb, and *Veronica officinalis*, a forest forb species. Trees with grass had four indicator species (5.4% of all species recorded in the seed bank of trees with grass), and all of them were ruderals (e.g., *Poa annua* and *Capsella bursa-pastoris*). Trees with shrubs harboured no indicator species. Forests had only one indicator species (1.8% of all species recorded in the seed bank of forests): a tall, grazing-sensitive forb of open habitats (*Hypericum perforatum*).

Species groups

In the herb layer vegetation of the three sites, we recorded a total of 349 plant species. The highest per plot richness was found under trees with shrubs, followed by open pastures, trees with grass and, finally, forests (Fig. 4a, Table S3). Grassland specialist species (183 in total) were the most numerous in open pastures, followed by trees with shrubs and trees with grass (Fig. 4c). Grassland species were nearly absent in the forests. Forest species (98 in total) showed similarly high richness in forests and under trees with shrubs, while trees with grass had fewer forest species, and open pastures had the lowest richness (Fig. 4e). Ruderal species (46 in total) were the most numerous under trees with grass (Fig. 4g). Trees with shrubs had fewer ruderal species, while forests and open pastures barely had any.

In the seed bank, we recorded 139 species. Their richness was similarly high under trees with grass and under trees with shrubs, while open pastures and forests had lower scores (Fig. 4b). Grassland species (82 in total) had similar richness in open pastures, trees with grass and trees with shrubs, and they were not absent in forests either, although were significantly scarcer than in the other three habitats (Fig. 4d). Forest species had similar richness under trees with grass and trees with shrubs, while open pastures and forests had lower richness levels (Fig. 4f). Ruderal species richness patterns were identical to those of the herb layer vegetation, with the highest scores under trees with grass, followed by trees with shrubs and similarly low values in forests and open pastures (Fig. 4h).

Discussion

In this study, we provide a new dimension to the understanding of vegetation patterns and dynamics of silvopastoral systems by comparing the herb layer vegetation to a so far neglected compartment, the soil seed bank. In line with our first hypothesis, the herb layer vegetation of the four main habitat types of the silvopastoral systems showed very

Table 3 Indicator species of the four habitat types (open pastures, trees with grass, trees with shrubs, and forests) in the herb layer vegetation and in the soil seed bank ($p < 0.01$)

HERB LAYER VEGETATION

Species	stat	*p*	Species	stat	*p*	Species	stat	*p*
Open pastures			**Trees with shrubs**			**Trees with shrubs (cont.)**		
Lotus corniculatus	0.885	0.001	*Crataegus monogyna*	0.891	0.001	*Ranunculus repens*	0.486	0.004
Festuca pseudovina/rupicola	0.814	0.001	*Fragaria vesca*	0.884	0.001	*Inula salicina*	0.456	0.004
Anthoxanthum odoratum	0.796	0.001	*Rosa canina* agg.	0.882	0.001	*Trifolium alpestre*	0.454	0.004
Hypochaeris radicata	0.773	0.001	*Veronica chamaedrys*	0.807	0.001	*Myosotis arvensis*	0.436	0.005
Draba verna	0.707	0.001	*Quercus petraea*	0.790	0.001	*Holcus lanatus*	0.484	0 006
Danthonia decumbens	0.672	0.001	*Prunus spinosa*	0.766	0.001	*Campanula patula*	0.468	0.006
Potentilla heptaphylla	0.669	0.001	*Clinopodium vulgare*	0.755	0.001	*Rumex acetosa*	0.447	0.006
Juncus tenuis	0.536	0.001	*Geum urbanum*	0.740	0.001	*Pyrus pyraster*	0.547	0.007
Centaurea jacea	0.596	0.002	*Brachypodium sylvaticum*	0.730	0.001	*Galeopsis tetrahit*	0.408	0.010
Carex caryophyllea	0.500	0.002	*Lysimachia nummularia*	0.722	0.001			
Carex tomentosa	0.511	0.004	*Torilis japonica*	0.643	0.001	**Forests**		
Polygala comosa	0.456	0.005	*Cruciata glabra*	0.634	0.001			
Centaurea phrygia agg.	0.480	0.008	*Veronica officinalis*	0.625	0.001	*Anemone nemorosa*	0.800	0.001
Inula britannica	0.449	0.010	*Viola hirta*	0.585	0.001	*Sanicula europaea*	0.609	0.001
			Euphorbia cyparissias	0.577	0.001	*Crocus heuffelianus*	0.593	0.001
Trees with grass			*Quercus robur*	0.572	0.001	*Acer pseudoplatanus*	0.577	0.001
			Vicia tetrasperma	0.540	0.001	*Oxalis acetosella*	0.540	0.001
Lolium perenne	0.935	0.001	*Carex pairae*	0.456	0.001	*Carex sylvatica*	0.517	0.001
Poa annua	0.880	0.001	*Trisetum flavescens*	0.483	0.001	*Fraxinus excelsior*	0.537	0.002
Polygonum aviculare	0.879	0.001	*Poa trivialis*	0.500	0.002	*Moehringia trinervia*	0.470	0.006
Veronica arvensis	0.872	0.001	*Quercus cerris*	0.478	0.002	*Lamium galeobdolon*	0.456	0.006
Capsella bursa-pastoris	0.842	0.001	*Cirsium vulgare*	0.521	0.003	*Chrysosplenium alternifolium*	0.456	0.009
Stellaria media	0.820	0.001	*Poa compressa*	0.484	0.003	*Lactuca muralis*	0.408	0.009
Geranium pusillum	0.675	0.001	*Hypericum perforatum*	0.483	0.004			
Sisymbrium officinale	0.500	0.002	*Galium mollugo*	0.479	0.004			

SEED BANK

Species	stat	*p*	Species	stat	*p*	Species	stat	*p*
Open pastures			**Trees with grass**			**Forests**		
Plantago lanceolata	0.735	0.001	*Poa annua*	0.780	0.001	*Hypericum perforatum*	0.442	0.008
Veronica officinalis	0.463	0.005	*Capsella bursa-pastoris*	0.727	0.001			
			Lolium perenne	0.581	0.001			
			Stellaria media	0.606	0.003			

distinct compositional patterns, confirmed by the PERMANOVA tests and visualised by the NMDS ordination. This is in line with previous studies that stress the effect of trees on micro-site conditions, such as shading, increasing nutrient content and altering soil moisture patterns compared to open pastures, and thus creating distinct niches within silvopastoral systems for organisms (Gea-Izquierdo et al. 2009, Fernandez-Moya et al., 2011, Hartel et al. 2013). A new addition to this well-established knowledge is that shrub encroachment under the trees gives rise to another distinct, although temporary, plant assemblage. The high between-habitat heterogeneity of the studied four habitat types highlights that each habitat has its conservation value in the landscape, and to preserve the overall rich flora of silvopastoral

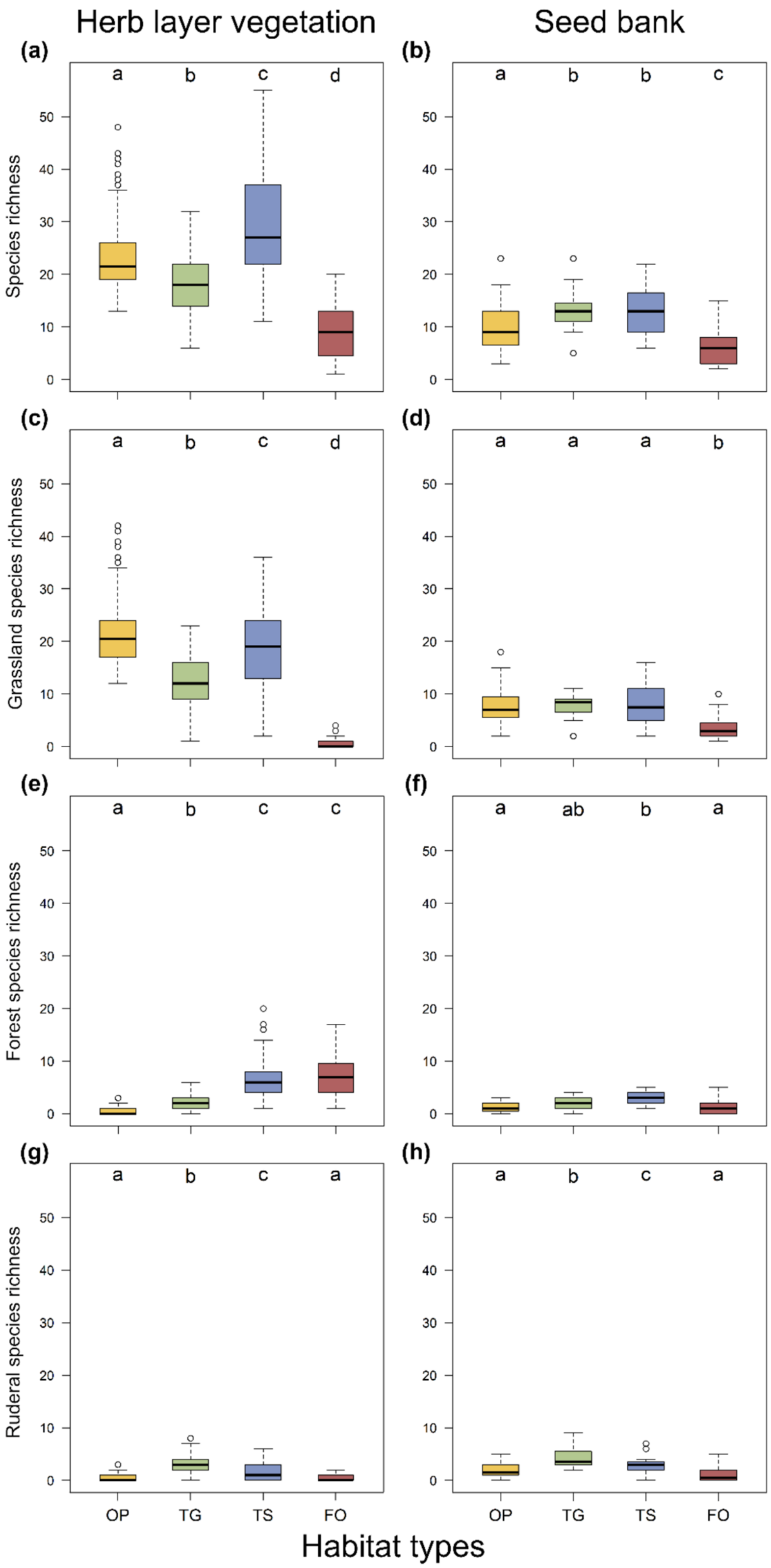


Fig. 4 Herb layer vegetation and soil seed bank species richness of the four habitat types. Different lowercase letters **a**–**d** indicate significant differences ($p < 0.05$) among habitat types (OP: open pastures, TG: trees with grass, TS: trees with shrubs, and FO: forests)

systems, we need all four habitat types, among which trees with shrubs, which have the lowest actual economic importance, have a prominent position.

Concerning the seed bank composition, habitat type had a significant effect according to the PERMANOVA tests but the habitats did not occupy as distinct areas in the ordination space as for the vegetation, and the between-habitat heterogeneity was significantly lower between habitat pairs in the case of the seed bank than in the herb layer vegetation. So, although just partly, our second hypothesis is also supported, and is in line with previous studies on various vegetation types that found greater compositional similarity in the seed bank across sites than in the aboveground vegetation (e.g., Bossuyt and Honnay 2008).

The large number of indicator species in the herb layer vegetation of the four habitats provided further support for the conservation importance of all four habitat types, but also revealed the prevailing environmental filters that lead to the compositional distinctness. Open pastures had species with adaptations to tolerate defoliation by grazing, while trees with grass had ruderal species that tolerate the high trampling disturbance by livestock congregating under the shade of the canopies. Forests, not surprisingly, had shade-tolerant forest specialists as indicators (Jakobsson et al. 2019). Finally, the transitional character of trees with shrubs led to a mix of various indicator species. In contrast, the seed bank of the habitats had very few indicator species, which is in line with the former compositional findings. Interestingly, trees with shrubs, which had the highest species richness and the highest number of indicator species in the herb layer vegetation, had no indicator species in the seed bank, whatsoever. This is also probably explained by its transitional position in the dynamics of silvopastoral systems, as even if their aboveground indicators build up a seed bank, it may remain in the soil after state transitions. The fact that seed banks represent a direct link between different compositional states of the herb layer is also highlighted by the only indicator of forests, which was a grassland specialist, and one of the two indicators of open pastures, which was a forest species.

Comparing the total species numbers and species groups in the aboveground vegetation and the seed bank helps us to understand further details of the dynamics (Fig. 5). Although the aboveground vegetation of trees with grass is not really species rich or valuable from a conservation point of view (see also Tölgyesi et al., 2018), this is an important input state for the soil seed bank. Through epi- and endozoochorous pathways livestock can import many grassland species besides the ruderal ones (Cosyns et al. 2005; Albert et al. 2015), so an easy compositional transition towards open pasture herb layer may be possible if a tree gets removed spontaneously or via human interference. If disturbance ceases for some time and shrubs take advantage, the grassland species can remain in the seed bank but forest species also increase. Forest-dwelling game and predators as well as various frugivorous birds may also use these patches (Röhrig et al. 2020; Simioni et al. 2022) and can assist zoochorous forest species (e.g., *Geum urbanum*). Furthermore, shrubs act as passive seed traps (Giladi et al., 2013), e.g., for anemochorous forest-dwelling Asteraceae species in our case, and dormant seeds of forest species, which bridged the non-forest states, can activate and proliferate. Forests and open pastures, as they represent end states, get enriched in their own species, but the seed bank preserves the footprint of past states, as forests still have grassland species in the seed bank, and grasslands do have forest ones, waiting for the environmental filters to change and speed up compositional transitions when activating from dormancy.

Unfavourable state transitions are the main threats to silvopastoral systems all over Europe and beyond, as traditional, extensive management is changing due to social-economic reasons, and both abandonment and intensification occur (Hartel et al. 2013, 2018). Abandonment favours forest regrowth via spontaneous succession, leading to the loss of herb layer species typical of open pastures, trees with grass and trees with shrubs (Oldén et al. 2017). Intensification often hinders shrub and hence tree recruitment (Herguido et al. 2017; Plieninger et al. 2021), and the lack of young tree cohorts coupled with a continuous loss of mature trees (often sped up by direct cutting; Hartel et al. 2018) favours open pasture species against the species of the other habitats. Trees with shrubs and trees with grass are among the losers of both pathways, so their associated herb layer species (particularly the non-ruderal indicators of trees with shrubs) and ecological functions (e.g., seed bank build-up under trees with grass) are the most threatened within silvopastoral systems and should

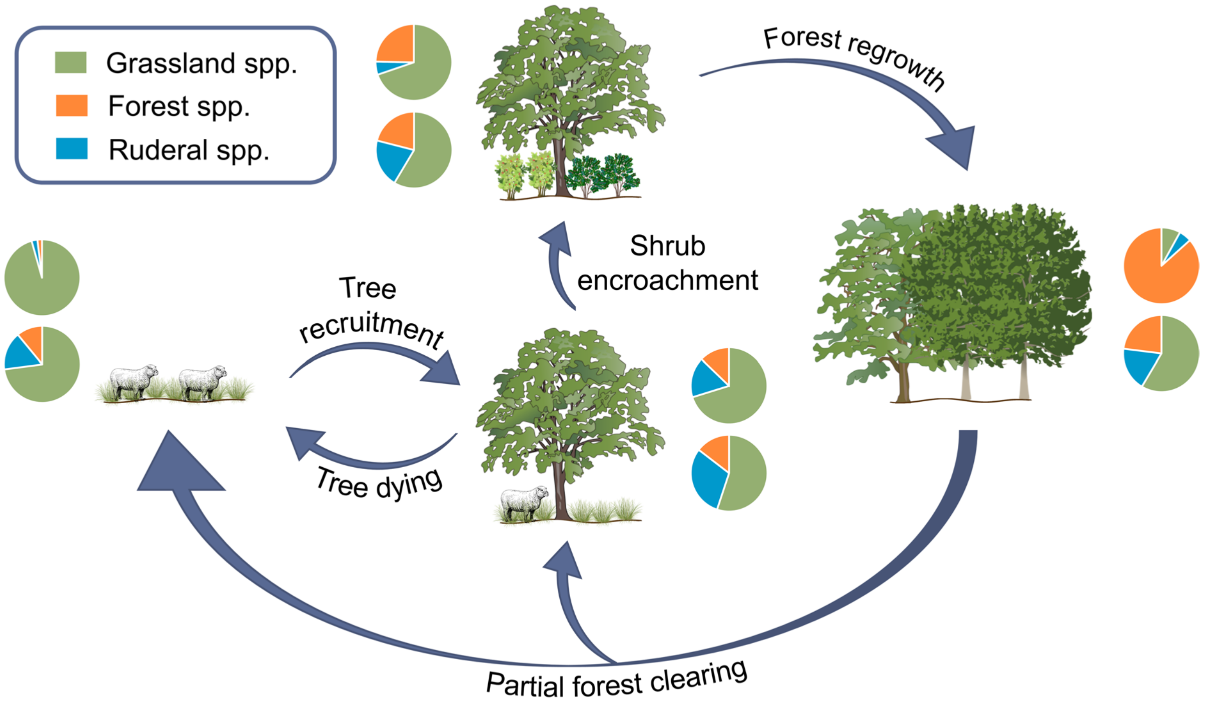


Fig. 5 Typical state transitions among habitats of temperate silvopastoral systems, which are accompanied by profound compositional transitions of the herb layer. Pie charts indicate the share of grassland specialist, forest specialist and ruderal plant species in the herb layer vegetation (upper charts) and the soil seed bank (lower charts). Images: http://ian.umces.edu/symbols/ and https://publicdomainvectors.org/

be recognised in conservation strategies. However, our study indicates that there might be a considerable resilience of the herb layer of every habitat to revert external degradation or unfavourable successional processes, as the seed bank is readily available to reactivate and turn the vegetation towards the desired state if the site conditions are reinstated. This is a promising precondition for the restoration of silvopastoral systems, whether they are intended to be implemented by thinning secondary forests (Rösch et al. 2019), increasing grazing pressure to revert excessive woody encroachment (Garrido et al. 2021), or applying grazing exclusion if tree recruitment is deficient due to intensive grazing pressure (Köbel et al. 2021).

Author contributions CT and PT conceived the study, CT, KF, AK, ZB, AAH, JS, RK, KT, KH, AV, BT and LE took part in data collection, KF and CT drafted the manuscript and all authors contributed critically to the final version.

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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