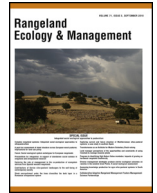




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Shrub Encroachment Under the Trees Diversifies the Herb Layer in a Romanian Silvopastoral System[☆]

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ABSTRACT

Rangelands with scattered trees are complex and dynamic systems with a long history in Europe. Generally referred to as “wood-pastures,” they are considered to have outstanding conservation value. Thorny shrubs are important for supporting the biodiversity of these wooded rangelands, as well as facilitating the regeneration of trees by acting as nurse species. We assess the direct effects of temporary shrub encroachment under the cover of mature sparse trees on overall plant and habitat diversity. We surveyed the herb layer of the main landscape features of a wood-pasture: open pasture, trees with a grass understory, trees with shrubs, and adjacent forest edges. The herb layer under trees with shrubs resembled that of forest edges more than open pastures and trees with grass. Trees with grass had a higher cover of ruderal species than trees with shrubs, while forest edges and open pastures had a lower cover of them. Forest species were absent from open pastures but were well represented in the other sites. The herb layer of trees with shrubs and forest edges had similar cover values, while trees with grass had a significantly lower cover of herbs than the other types. Trees with shrubs had higher species richness than any of the other three landscape features and had a much higher proportion of diagnostic species. We conclude that the scattered trees and shrubs of the studied silvopastoral system have additive facilitative effects on their understory, probably through modifying the microenvironment and grazing pressure, leading to the formation of temporary diversity hot spots with distinct vegetation. Thus maintaining a moderate level of shrub-encroachment under sparse trees is recommended for not only creating safe havens for tree recruitment but also increasing the overall species and habitat diversity of wood-pastures.

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Introduction

Silvopastoral systems are among the most ancient land-use forms, with the earliest known examples dating back to the Neolithic (Mosquera-Losada et al., 2009; Bergmeier et al., 2010; Hartel et al., 2013). They can have a range of physiognomies from closed canopy grazed forests to “savanna-like” open woodlands (Rackham, 1980). The focus of our research is on the savanna type of wooded rangeland (or as referred to in Europe, wood-pasture) system, where the landscape is dominated by grassland and the trees are sparsely distributed.

Scattered trees in these wooded rangelands are keystone structures as their ecological role is disproportionately large relative to their spatial extent (Manning et al., 2006; López-Sánchez et al., 2016). The trees and other woody vegetation break up the structural homogeneity of open pastures and provide microhabitat for a variety of organisms otherwise not typical of grasslands (Lindenmayer, 2017). Several forest-specific plants can thrive under the canopy of scattered trees (Bergmeier et al., 2010), various woodland birds use them as feeding and nesting places (Tucker and Evans, 1997; Hartel et al., 2014), and the trees sometimes host more forest invertebrates, especially saproxylic insects, than adjacent forests (Sebek et al., 2016). As a result, wood-pastures may harbor a significantly higher biodiversity than either treeless pastures or closed forests (Plieninger et al., 2015).

Besides their outstanding conservation role, scattered trees provide a variety of ecosystem services (Hartel et al., 2013; Hartel and Plieninger, 2014; López-Santiago et al., 2014). Their canopy gives shelter for the grazing livestock from the heat of the sun (Higgins and Dodd, 1989), and their foliage is also used for fodder, especially in drought conditions, when forage yield is low (Varga et al., 2015). Fruits,

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like acorns, are an important supplementary food source for grazers, while the trees are also sources of timber, harvested mostly by pollarding (Rackham, 1980; Kirby et al., 1995).

Taking all the ecological and economic benefits of scattered trees into account, wood-pastures are among those land use forms where humans and nature can still mutually profit in a sustainable fashion (Bignal and McCracken, 1996; Plieninger, 2007). Despite this, their long-term survival is uncertain. Wood-pastures are forced into the categories of forest or pasture by policymakers, but the multifunctional system of wood-pasture rarely exists as a legal category and therefore often remains unprotected. As a result socioeconomic trends like intensification of livestock production through tree removal or land abandonment threaten wood-pastures all over Europe (Manning et al., 2006; Bergmeier et al., 2010). Similarly to other extensive land-uses like hay meadows, pastures, and orchards, both intensification and abandonment can have negative effects. If grazing intensity is too high in wood-pastures, tree recruitment is hindered, leading to a decrease of tree cover in the long run (Gillet et al., 1999; Dimopoulos and Bergmeier, 2004). Conversely, underuse leads to shrub and subsequent tree encroachment, and finally conversion to forest (Gillet et al., 1999; Miklín and Cizek, 2014), leading to the decline of the ecological and agricultural benefits described earlier (Plieninger et al., 2015).

Shrub encroachment is a typical indicator of underuse not only in wood-pastures but also in many seminatural (grazed or mowed) grassland types of economic importance (MacDonald et al., 2000; Eldridge et al., 2011). However, shrubs have a crucial role in wood-pastures, as

they serve as nurse plants for tree saplings by protecting them from grazers (Callaway, 1995). A certain amount of shrub cover is, thus, vital to sustain tree regeneration in pace with tree mortality. At the same time, shrubby patches also represent a third type of landscape features in these rangelands, so the question arises of whether they have other effects on the diversity and conservation value of wood-pastures besides allowing for tree regeneration.

The purpose of this study was to characterize the herb layer of trees with shrub-encroached undergrowth in an extensively used Romanian wood-pasture. Specifically, we asked the following three questions: 1) Does the herb layer composition differ among the four main landscape features (i.e., open pasture surfaces, scattered trees with a grassy understory, shrub-encroached scattered trees, and the ecotone between the wood-pasture and adjacent forest?) 2) What successional changes (with a special focus on ruderal and forest-specific species) take place once the understory is encroached upon by shrubs? 3) Do such successional foci add any extra conservation value to the wood-pasture, or are shrubs only needed for tree regeneration?

Materials and Methods

Study Site

The study was carried out in central Romania near the village of Deusu (N46.92 E23.50, 420–480 m a.s.l.), 15 km to the north of Cluj-Napoca (Fig. 1). The climate is continental with a mean annual

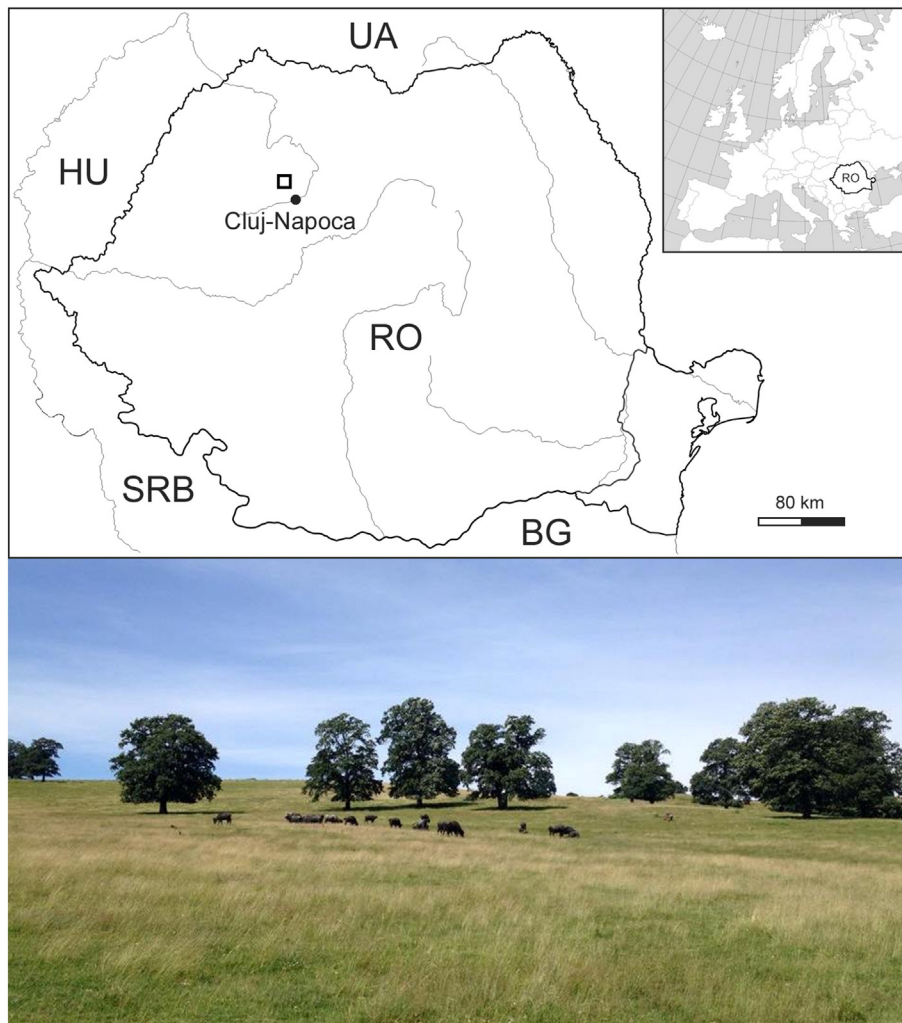


Figure 1. Location of the studied wood-pasture (empty square) near Cluj-Napoca (black circle) in NE Romania and its general physiognomy.

precipitation of 600 mm and a mean annual temperature of 8.3°C. The area is hilly with gentle slopes; the soil is loamy with a deep humus-rich upper stratum. The potential vegetation is oak-hornbeam forest, but there is a 250-ha confluent area where the typical land use is wood-pasture. This area with scattered trees was selected for our study. The creation of this wood-pasture presumably dates back to the 18th century or earlier (Hartel et al., 2015) and is typical of the lowland-hilly parts of northwestern and central Romania. Tree density for the overall surface is around 1 tree ha⁻¹. Most trees are oaks (*Quercus petraea*, *Quercus cerris*, and *Quercus robur*), but some large hornbeams (*Carpinus betulus*) and wild pears (*Pyrus pyraeaster*) also occur.

Grazing intensity in the area is moderate (0.9–1.1 livestock units ha⁻¹ per yr) (local shepherds, personal communication). The main livestock species include cattle and buffalo (between May and November), but sheep grazing also takes place (all-yr round). Animals frequently find shelter under the shade of the trees; therefore, the consequences of their presence (trampling, manure, etc.) are more concentrated under the tree canopy than in the open pasture. However, the understory of several sparse trees has been invaded by thorny shrubs like *Crataegus monogyna* and *Prunus spinosa*. Shrubby areas are less attractive to livestock and are less influenced by them.

Data Collection

Forty sites were selected using a stratified random design (Fig. 2). Sites were located > 100 m apart to ensure spatial independence. Each site consisted of three 1-m² quadrats resulting in a total of 120 quadrats in the study (see later for further details). Preliminary surveys revealed that some scattered trees have shrubs under their canopy, while others do not. Therefore, we included the shrubs under the canopy as a category, resulting in 10 sites with sparse trees with shrubs under the canopy (hereafter “trees with shrubs”) and 10 sparse trees without shrubs under their canopy (hereafter “trees with grass”). Previous field experiences and interviews with local shepherds suggested that the shrub encroachment under the tree canopy was the result of a drop in grazing intensity in these specific microenvironments in the past decade. Decreased grazing intensity is well known to trigger invasion of woody vegetation on pastures (e.g., Garbarino et al., 2012; Smit

et al., 2015; Oldén et al., 2016). We selected mature oak trees with a diameter at breast height of 70–100 cm because these were the dominant trees on this wood-pasture.

In order to capture the full gradient of fine-scale environmental heterogeneity provided by woody vegetation, we also selected 10 open pasture sites (situated > 50 m from the closest tree, hereafter “open pastures”) and 10 sites along the edges of the adjacent oak-hornbeam forests (i.e., in the ecotone between the wood-pasture and forest, hereafter “forest edges”). Forest edges also contained shrubs but fewer than the trees with shrubs sites. Only relatively flat sites were selected to avoid the confounding effect of slope exposure.

Vegetation surveys took place in July 2015. The quadrats for trees with grass and trees with shrubs were located approximately 2–3 m from the trunk of the trees, in the vertices of equilateral triangles. The quadrats for open pastures were arranged in a similar configuration but with no tree in the center. For forest edges, the three quadrats were aligned 2–3 m pasture-wards from the outermost tree trunks to capture the specific microenvironment represented by the forest edge (see Fig. 2). All vascular species in the quadrats were identified to the species level and were assigned a cover value in percent. Saplings of trees and shrubs were included as understory only if they were shorter than 50 cm.

Data Analysis

As a preliminary check, we tested the dataset for spatial autocorrelation with Mantel’s test, in which we correlated the Euclidean distance of the sampling sites with their Bray-Curtis compositional dissimilarities (after averaging the three relevés per sampling site). The test had a significant result ($z = 4.55$, $P = 0.04$) but this was caused by the fact that forest edges on one side of the wood-pasture had similar sun exposures that were different from those on the opposite side (i.e., autocorrelation was secondary to exposure, which was taken into account for the interpretation of results). After excluding forest edges from the Mantel test, the result was no longer significant ($z = 2.04$, $P = 0.13$).

The compositional similarity of the studied landscape features was assessed with nonmetric multidimensional scaling (NMDS). For the analysis, we averaged the relevé triplets for each sampling site and used the resulting 40 records. After square root transformation of the data, we applied the Bray-Curtis dissimilarity and made the calculations using two NMDS axes. To understand what lies behind these compositional patterns, we prepared linear models for two pivotal species groups, ruderal and forest species. Ruderal species were considered because they are associated with disturbance (a potential negative effect of grazing and trampling) and are disadvantageous from a conservation point of view. Conversely, the presence of forest species adds extra conservation value to pastures dominated by grassland species, and processes of forest regeneration under trees with shrubs may be expected to alter their amount. Ruderal and forest species were identified according to habitat fidelity to ruderal and woody communities, respectively, using the classification of Sârbu et al. (2013). Ruderal and forest species recorded during the study are identified in Table S1 (available online at <https://doi.org/10.1016/j.rama.2017.09.004>).

Ruderal species were absent in several quadrats, leading to zero-inflation in the dataset; therefore, we averaged the three relevés per sampling site, and after square root transformation we could build a generalized linear model (GLM) with a Gaussian error term. In the case of forest species, there was no need for the averaging of the relevé triplets, but we prepared a generalized linear mixed-effects model (GLMM) with site as the random factor. We applied square root transformation and Gaussian error term here, too. Open pastures contained a negligible cover of ruderal species and no forest species; therefore, open pastures were excluded from these analyses. Tree and shrub species recorded in the relevés were excluded from the analysis of forest species because they do not have a preference for forest communities, but they make them forest communities.

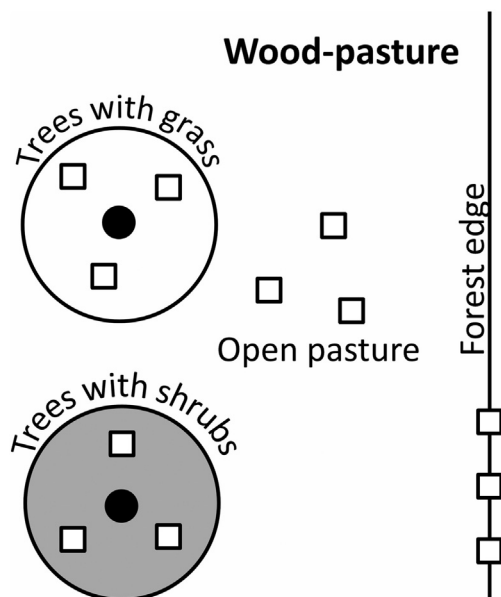


Figure 2. Illustration of the study design. Large and small circles are the projections of tree canopies and the tree trunks, respectively. Sampling quadrats (empty squares) of the herb layer vegetation of trees were placed 2–3 m from the trunk, in the vertices of equilateral triangles. Quadrats in the open pasture sampling sites had a similar configuration, while the quadrat triplets in the forest edges were aligned in a line. Each of the four landscape features had 10 replicates.

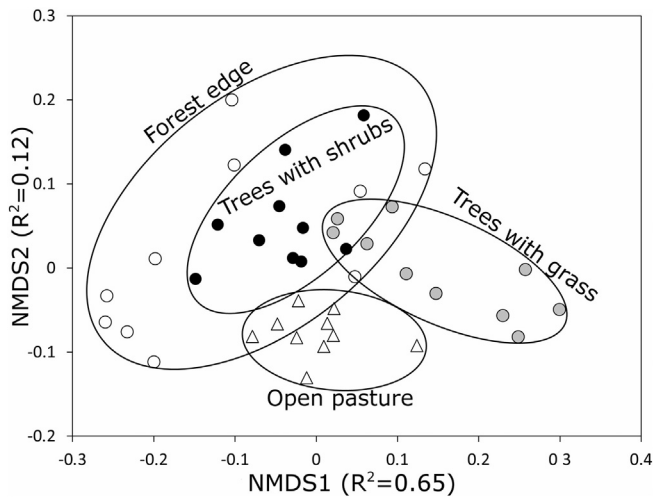


Figure 3. NMDS ordination of the herb layer of the typical landscape features of the studied wood-pasture. The three relevés of each site were averaged, resulting in 10 data points for each type of site. Stress factor: 0.181.

We also examined species richness by calculating a GLMM with Poisson error term on the untransformed species richness values of the relevés. Finally, we identified diagnostic species for each landscape feature. Diagnostic species are those that show high fidelity to certain vegetation units (Chytrý et al., 2002). Fidelity measures are frequently used tools for identifying such species (Tichý and Chytrý, 2006; Willner et al., 2009); they compare observed species frequencies within vegetation units with frequencies that would be expected if the species were randomly distributed among different vegetation units (Bruehlheide, 2000; Chytrý et al., 2002). In this study, phi-values of fidelity were calculated and nonsignificant diagnostic species were excluded with Fischer's exact test (Tichý and Chytrý, 2006).

The ordination and models were calculated in an R environment (R Core Team, 2013) using the *vegan* (Oksanen et al., 2011) and *lme4* (Bates et al., 2011) packages, respectively. The significance of the GLM was assessed with the analysis of variance function of the *stat* package, while that of the GLMMs was calculated by comparing the models with null models containing only the random factor. Post hoc sequential comparisons among factor levels were assisted with the *relevel* function and the FDR method was applied to correct the *P* values. Significance level was set to $P = 0.05$ in all analyses.

Results

According to the NMDS, the herb layer of open pastures and trees with grass occupied distinct regions in the ordination space. Forest edges had rather diverse vegetation, entirely encompassing the assemblages of trees with shrubs and slightly overlapping with the open

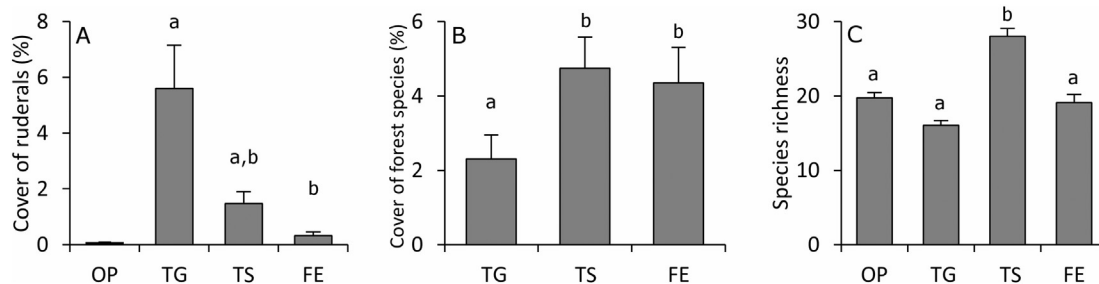


Figure 4. Percentage cover of ruderal species (A) and forest species (B) and the species richness of the studied landscape features. Different lower case letters indicate significantly different groups ($P < 0.05$); error bars show the standard error of the mean. OP: open pasture, TG: trees with grassy undergrowth, TS: trees with shrubby undergrowth, FE: forest edges. OP was excluded from panel B because forest species did not occur in the open pasture.

Table 1

Comparisons of the cover of ruderal and forest species and the species richness of the four main landscape features of the studied wood-pasture using the fitted models. *P* values were corrected with the FDR method.

	Ruderal species		Forest species		Species richness	
	<i>t</i>	<i>P</i>	<i>t</i>	<i>P</i>	<i>z</i>	<i>P</i>
TG vs. TS	−1.867	0.073	−3.240	0.009*	6.19	< 0.001*
TG vs. FE	−2.483	0.019*	−2.663	0.026*	1.49	0.164
TS vs. FE	−0.616	0.543	0.576	0.569	−4.32	< 0.001*
OP vs. TG	−1.95	0.077
OP vs. TS	3.84	< 0.001*
OP vs. FE	0.47	0.640

TG indicates trees with grass; TS, trees with shrubs; OP, open pasture; FE, forest edge.

* $P < 0.05$.

pastures and trees with grass. Trees with shrubs showed practically no overlap with trees with grass and open pastures (Fig. 3).

A total of 24 ruderal species were detected in the relevés; the most abundant species were *Poa annua*, *Polygonum aviculare*, and *Stellaria media*. The GLM was significant ($F = 3.34$, $P = 0.050$) and indicated that trees with grass had a significantly higher overall coverage of ruderal species than forest edges. However, only marginal significance was found between trees with grass and trees with shrubs. Furthermore, no significant difference was found between the ruderal species cover in trees with shrubs and that of forest edges (Fig. 4A, Table 1).

We recorded a total of 32 forest species, of which *Helleborus purpurascens*, *Luzula luzuloides*, and *Veronica officinalis* were the most abundant. According to the GLMM of forest species (*Chi-square* = 8.03, $P = 0.018$), trees with shrubs and forest edges had similar amounts of forest species, while trees with grass had a significantly lower cover of forest species in the herb layer (see Fig. 4B, Table 1).

The total number of species recorded in the study was 195 (Table S1; available online at <https://doi.org/10.1016/j.rama.2017.09.004>). The greatest number of species was found under trees with shrubs (145), followed by forest edges (129). Trees with grass and open pastures had a similar but lower total number of species (82 and 87, respectively) than the other types. The GLMM of species richness was significant (*Chi-square* = 32.32, $P < 0.001$) and yielded a pattern similar to the total species numbers. Trees with shrubs had significantly higher values than any of the other types, which, in turn, did not differ from each other (see Fig. 4C, Table 1).

The analysis of diagnostic species (Table 2) revealed that open pastures harbored 23 species with significant fidelity. These were mostly grazing-tolerant grasses (like *Cynosurus cristatus*), short, rosette-forming dicots (like *Leontodon* spp.) and legumes typical of mesic pastures (e.g., *Lotus corniculatus* and *Trifolium pratense*). Species specific to trees with grass included only disturbance-tolerant and ruderal species (like *Capsella bursa-pastoris* and *Poa annua*); their total number was 11. Forest edges had 19 diagnostic species, consisting of a mixture of low-growing, grazing-tolerant species (e.g., *Prunella laciniata* and *Veronica prostrata*) and taller, more grazing-sensitive forbs

Table 2
Significant diagnostic species and their phi-values in the four types of sites in the studied wood-pasture.

Open pasture		Trees with grass		Trees with shrubs				Forest edges	
Species	phi	Species	phi	Species	phi	Species	phi	Species	phi
<i>Cynosurus cristatus</i>	57.2	<i>Capsella bursa-pastoris</i>	55.0	<i>Vicia tetrasperma</i>	45.3	<i>Cirsium vulgare</i>	23.1	<i>Pimpinella saxifraga</i>	56.6
<i>Trifolium pratense</i>	42.6	<i>Polygonum aviculare</i>	49.5	<i>Crataegus monogyna</i>	44.3	<i>Agrimonia eupatoria</i>	22.5	<i>Trifolium ochroleucon</i>	46.3
<i>Trifolium repens</i>	42.4	<i>Lolium perenne</i>	43.6	<i>Galium verum</i>	41.5	<i>Carex spicata</i>	22.2	<i>Arenaria serpyllifolia</i>	38.6
<i>Lotus corniculatus</i>	40.7	<i>Geranium pusillum</i>	41.8	<i>Veronica officinalis</i>	41.3	<i>Trisetum flavescens</i>	22.1	<i>Centaurea phrygia</i> agg.	38.5
<i>Carex hirta</i>	39.7	<i>Taraxacum officinale</i>	41.0	<i>Vicia angustifolia</i>	39.7	<i>Aphanes arvensis</i>	21.4	<i>Thymus glabrescens</i>	33.7
<i>Danthonia decumbens</i>	39.6	<i>Poa annua</i>	38.5	<i>Rosa canina</i> agg.	37.8	<i>Filipendula vulgaris</i>	21.4	<i>Prunella laciniata</i>	30.9
<i>Luzula campestris</i>	39.3	<i>Stellaria media</i>	35.0	<i>Galium mollugo</i>	37.3	<i>Pilosella piloselloides</i>	21.4	<i>Veronica prostrata</i>	29.4
<i>Achillea millefolium</i>	38.3	<i>Bromus hordeaceus</i>	34.9	<i>Calamagrostis epigejos</i>	36.1	<i>Viola hirta</i>	21.4	<i>Inula</i> sp.	28.3
<i>Trifolium dubium</i>	33.7	<i>Ranunculus bulbosus</i>	27.7	<i>Viola canina</i>	35.5	<i>Festuca valesiaca</i>	20.7	<i>Rorippa pyrenaica</i>	27.7
<i>Cerastium pumilum</i>	31.8	<i>Sisymbrium officinale</i>	27.7	<i>Veronica chamaedrys</i>	33.9	<i>Campanula patula</i>	20.1	<i>Fragaria viridis/vesca</i>	27.2
<i>Carex leporina</i>	27.7	<i>Plantago major</i>	23.2	<i>Prunus spinosa</i>	32.3	<i>Geum urbanum</i>	18.9	<i>Luzula divulgata</i>	26.5
<i>Cuscuta</i> sp.	27.7			<i>Euphorbia cyparissias</i>	31.7	<i>Cruciata pedemontana</i>	18.0	<i>Potentilla erecta</i>	26.5
<i>Festuca stricta</i>	27.7			<i>Lychnis viscaria</i>	30.9	<i>Daucus carota</i>	17.8	<i>Helianthemum nummularium</i>	23.1
<i>Polygala vulgaris</i>	27.7			<i>Trifolium medium</i>	30.9			<i>Cytisus nigricans</i>	22.1
<i>Deschampsia cespitosa</i>	26.5			<i>Agrostis capillaris</i>	30.4			<i>Hypericum perforatum</i>	21.7
<i>Euphrasia stricta</i>	26.5			<i>Anthoxanthum odoratum</i>	28.8			<i>Hieracium murorum</i>	21.4
<i>Leontodon hispidus</i>	25.7			<i>Festuca rubra</i>	28.2			<i>Silene nutans</i>	21.4
<i>Plantago lanceolata</i>	25.7			<i>Linaria vulgaris</i>	27.7			<i>Trifolium campestre</i>	19.2
<i>Leontodon autumnalis</i>	24.0			<i>Ajuga genevensis/reptans</i>	26.7			<i>Potentilla argentea</i>	17.8
<i>Potentilla reptans</i>	21.4			<i>Dianthus armeria</i>	26.7				
<i>Sagina subulata</i>	21.4			<i>Genista tinctoria</i>	24.2				
<i>Potentilla heptaphylla</i>	20.7			<i>Lysimachia nummularia</i>	24.1				
<i>Prunella vulgaris</i>	20.5			<i>Ranunculus polyanthemos</i>	24.0				

(e.g., *Centaurea phrygia* and *Hypericum perforatum*), some of which show a high fidelity to dry oak forests (e.g., *Cytisus nigricans* and *Hieracium murorum*). Trees with shrubs hosted the highest number of diagnostic species (36 species, equal to 18.5% of the total species pool of the landscape). These species included all sorts of species groups like ruderal species (e.g., *Cirsium vulgare*); short, grazing-tolerant species (e.g., *Ajuga genevensis* and *Lysimachia nummularia*); taller, grazing-sensitive species (e.g., *Galium mollugo* and *Linaria vulgaris*); as well as forest species (*Veronica officinalis* and *Geum urbanum*). There were also three spiny shrubs among the diagnostic species of trees with shrubs, including *Crataegus monogyna*, *Rosa canina* agg., and *Prunus spinosa*.

Discussion

We found that open pastures, trees with grass, and trees with shrubs had distinct plant assemblages. The difference between trees with grass and open pastures is in line with previous studies that emphasized the floral distinctness of these fine-scale structural elements (Armas et al., 2011; Fernández-Moya et al., 2011). Sparse trees create special micro-environmental conditions in their close vicinity. For example, their canopy intercepts solar radiation resulting in shadier, cooler, and often moister conditions (Vetaas, 1992; Gillet et al., 1999). This microclimatic difference may have enabled the colonization of forest species under trees but not in the open pastures, which is a form of facilitation, a positive plant-plant interaction between trees and forest species. Trees can also lead to higher nutrient concentrations under their canopy due to litter decomposition, root turnover, and, most importantly, manure concentrations (Rhoades, 1997; Manning et al., 2006). In our pasture system, we also detected clear signs of livestock activity (i.e., trampling and manure) under every tree with a grassy understory. The higher level of disturbance and nutrients was well reflected in the higher ruderal cover under trees with grass compared with the open pasture and by the fact that the diagnostic species of trees with grass were all ruderal species.

The floral composition under trees with shrub-encroached understory is not frequently examined in studies of savanna-like rangelands. In some respects, shrubs can have similar effects on the microenvironment as those of trees, as has been shown for *Retama sphaerocarpa*, a leguminous shrub in Iberian wood-pastures known as dehesas (Armas et al., 2011; Rolo et al., 2014). There is, however, a major difference

between sites that have trees with shrubs and those with a grassy understory when it comes to livestock grazing. The main shrub species on our sites were *Prunus spinosa* and *Crataegus monogyna*; both have pronounced thorns. It has been shown that the presence of thorny shrubs can reduce grazing pressure (Bakker et al., 2004). The presence of thorny shrubs and the resulting low livestock activity probably favored the establishment of forest species and a slight (only marginally significant) decrease in ruderal species. As a result of these micro-environmental differences, trees with shrubs sites became similar to forest edges. They are examples of “all-edge” patches, which are too small to have distinct edge and interior zones. The importance of such ecotone-like formations in wood-pastures is emphasized by Bergmeier et al. (2010), who attribute key roles to them in increasing niche and overall species diversity.

Trees with shrubs occupied a more compact region in the ordination space than forest edges. We interpret this result as a potentially higher variation in the sun exposure of forest edges compared with trees with shrubs. The importance of sun exposure in shaping ecotone assemblages was also emphasized by Erdős et al. (2013), who showed that south- and north-facing forest edges have systematic differences in their floral composition, which also appeared in our dataset in the form of some autocorrelation (see “Data Analysis” earlier). We also found some more notable differences between trees with shrubs and forest edges. The release from the effect of herbivores led to a significant increase in species richness (at least for the short term) under trees with shrubs, making them the most diverse landscape features in the studied wood-pasture. This high density of species can be only partly explained by the increase in forest species coupled with a delay in the decrease of ruderal species. The analysis of diagnostic species proved that there were several species typical only of this kind of site. Moreover, the number of such species was outstandingly high. These results suggest that the effect of trees and shrubs on understory vegetation could be additive.

Facilitation, however, is not the only plant-plant interaction trees and shrubs can have on the undergrowth; it has been shown that competition can also be important (Callaway and Walker, 1997). Depending on the availability of resources and the climatic context, competition can exceed facilitation and the net effect of woody species can become negative on certain parameters (like productivity or diversity) of the understory assemblages (Belsky, 1994; Gea-Izquierdo et al., 2009). For this reason, the combined effect of trees and shrubs could be expected

to be competitive or neutral, so the net positive effect we found needs more explanation.

Net negative interactions are found mostly in arid regions, where competition for water exceeds the positive effect of increased nutrient availability and the temperature-ameliorating effect of shading (Holmgren et al., 1997; Maestre et al., 2005). This is especially true if the woody species have a superficial root network, like the shrub *Cistus ladanifer* in Iberian dehesas (Rivest et al., 2011) or when the soil is sandy and has a low water-holding capacity (Gea-Izquierdo et al., 2009). In our situation, water is not especially a limiting factor, and our shrubs and trees have deep taproots, leading to spatial resource partitioning of soil moisture among trees, shrubs, and herb layer species.

Competition for light can also be a limiting factor in some wood-pasture types and can lead to net competition (Maranón and Bartolome, 1994; Gea-Izquierdo et al., 2009). Although light interception is obviously higher in our trees with shrubs than in the ones with grass, the regional pool of herb layer species contains a large variety of shade-tolerant forest plants because the region belongs to an oak-hornbeam forest belt and these forests are well preserved in large areas (Hartel et al., 2013). Thus, there is a substantial source of shade-tolerant species, which is not necessarily the case in other places. As a generalization of the previously mentioned constraints on facilitation, the net effect of plant-plant interactions depends on the most limiting factor (Belsky, 1994; Brooker et al., 2008). This factor may not only be light or water but also the intensity of herbivory. Our findings suggest that in our silvopastoral system, herbivory was a stronger constraint than the shading effects and moisture demands of trees and shrubs.

The outlined protective effect of shrubs on understory species applies for tree saplings as well (Hartel et al., 2013; Rolo et al., 2013). Shrubs are concentrated under the canopy of mature trees, probably because of the increased seed rain by frugivorous birds (like *Turdus* spp.), which frequently roost on sparse mature trees (Sorensen, 1981) and because of the positive effects of trees on shrub survival as compared with open pastures (cf. Smit and Ruifrok, 2011). As a consequence of the association of shrubs with mature trees, tree regeneration is also more typical under (and in the near vicinity of) mature trees while virtually no tree regeneration occurs in the open pasture. It would be more favorable if shrubs could colonize in open pastures, leading to a more even spatial distribution of trees. A considerable reduction of grazing pressure in some yrs (e.g., grazing exclusion) may lead to windows of opportunity for shrub colonization on the open pasture parts (Plieninger, 2007; Smit et al., 2010), which should be promoted among land users. This would not only allow for an improved tree recruitment pattern but also lead to the formation of another landscape feature, treeless shrub stands, potentially with another type of herbaceous undergrowth and an even higher overall diversity.

Conclusions and Insights for Management

Shrubs are necessary components of many wooded rangelands because they serve as nurse plants for tree recruitment (Hartel et al., 2013; Rolo et al., 2013). In our study we also demonstrated that they can have beneficial effects on the understory, leading to a unique, species-rich herb layer, which lends extra conservation value to these landscapes. Trees with shrubs had higher species richness than any of the other three types and had a much higher proportion of diagnostic species. We conclude that the scattered trees and shrubs of the studied silvopastoral system have additive facilitative effects on their understory, probably through modifying the microenvironment and grazing pressure, leading to the formation of temporary diversity hot spots with distinct vegetation. This diversifying effect of shrubs should also be taken into account when planning the management and conservation of wood-pastures. Trees with shrub-encroached undergrowth are transitional phases from grassland to forest, which can be maintained only by fine-tuning management practices. As transitional phases, they should not be conserved in single locations within a rangeland

but rather rotated through different locations over time. Overgrazing and excessive shrub clearing reduce shrub cover, but a too-low intensity of land use can allow encroachment to progress and cause widespread conversion to forest. Thus, the generally recommended (and also traditionally applied) intermediate grazing intensity can be used to promote sparser tree recruitment and maximize overall plant diversity at the same time.

Many Eastern European rangelands went through periods of land abandonment due to the institutional and socioeconomic changes of the past decades. These periods of abandonment of grazing always resulted in shrub encroachment (authors, personal observation in > 100 silvopastoral systems) and could be used as unique opportunities for cost-effective regeneration of trees in these systems. The management of silvopastoral systems such as the one presented in this paper is currently regulated under the Common Agricultural Policy and national level forestry authorities. None of these formal regulations explicitly promote the regeneration of trees on grazing lands. Nevertheless, we highlight that within the current silvopastoral system, the encroachment of shrubs happens mostly under mature tree canopy. If the maintenance of large, mature, and light-demanding trees (e.g., oaks) is also a biodiversity conservation priority, strategies should include the selective removal of young trees that are growing too densely and too close to mature trees and encouraging regeneration of scattered trees in the grasslands instead. Maintaining a moderate level of shrub encroachment under sparse trees is recommended for not only creating safe havens for tree recruitment but also increasing the overall species and habitat diversity of wood-pastures.

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