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Maintaining scattered trees to boost carbon stock in temperate pastures does not compromise overall pasture quality for the livestock

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ABSTRACT

Scattered trees in wood-pastures represent outstanding conservation value by providing microhabitats for a variety of organisms. They also diversify ecosystem services by creating shade for livestock, and capturing and storing carbon. However, trees in wood-pastures are declining Europe-wide and an appropriate legal environment to maintain them is mostly lacking. Here we looked beyond the well-documented beneficial effects of trees and assessed potential ecosystem disservices, which may drive the controversial appreciation of trees. In a grazing exclusion experiment, we assessed the effect of trees on herbage production in wood-pastures from semi-arid continental to humid montane areas in the temperate deciduous forest ecoregion, and found that trees have a suppressive effect throughout the year, although herbage nutritive value, as indicated by herbage nitrogen content, seems to be improved in spring. When we up-scaled the local ecosystem disservice on herbage yield to entire wood-pastures, the loss remained below 3%, which is lower than reported gains in livestock production due to free access to shade. Thus, the motivation for the under-appreciation of trees by land managers and decision makers may lie in that trees suppress herbage production, but the importance of this effects is offset by the magnitude of the beneficial services of trees. We recommend current wood-pasture stakeholders to revisit their attitude towards scattered trees and encourage tree planting campaigns and tree-based climate mitigation strategies to consider the protection of trees in wood-pastures and the establishment of young ones in currently open pastures up to traditionally low tree cover proportions, as livestock production is unlikely to be compromised by this action.

1. Introduction

Climate change is among the most imminent threats to present-day human societies (Auffhammer, 2018; IPBES, 2019; Pörtner et al., 2022). It can be tackled by reducing greenhouse gas emissions and removing excess amounts from the atmosphere (Walker et al., 2022). The latter has been globally synonymized with tree planting, as trees can capture and store large quantities of carbon in their trunks, branches and roots. In line with this, large areas have been subjected to tree planting globally (Bond et al., 2019; Di Sacco 2021; Li et al., 2021). Advocates of open ecosystems (i.e. grasslands and sparsely wooded ecosystems) have raised many concerns against this simplification (e.g. Bond et al., 2019; Veldman et al., 2019), as tree planting projects often target naturally open ecosystems or cultural landscapes, such as traditionally/extensively managed ancient grasslands, which possess high biodiversity and ecosystem service provisioning capacity, often including significant carbon capturing and storing potential in their soil (Bond et al., 2019; Temperton et al., 2019; Tölgyesi et al., 2022).

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The decision between forest and open ecosystem, however, should not be narrowed down to a binary solution. Scattered woody vegetation in open landscapes introduces environmental heterogeneity (Belsky et al., 1993), leading to a great increase in overall biodiversity and a diversification of ecosystem services (Manning et al., 2006, 2009; López-Sánchez et al., 2016; Erdős et al., 2018). Therefore, a mild to moderate level of tree planting or preserving already present trees in open ecosystems may lead to overall beneficial effects, reconciling interests of tree planting groups and advocates of open ecosystems. However, the appropriate balance is a matter of debate, as there can be strong trade-offs among the ecosystem services of forested and open ecosystems (e.g. Jackson et al., 2005).

An epitome of mixed landscapes composed of woody and grassy parts is represented by wood-pastures, commonly found in many European (Bergmeier et al., 2010; Plieninger et al., 2015) and North- and South-American countries (Neel and Belesky, 2017; Calle, 2020), as well as in Australia (Fischer et al., 2010). Wood-pastures are considered among the most ancient and biodiverse cultural landscapes (Bergmeier et al., 2010; Hartel et al., 2014). They reportedly harbor higher bird, bat, arthropod and plant diversity than either treeless pastures or closed-canopy production forests (Hartel et al., 2014; López-Sánchez et al., 2016; Gallé et al., 2017; Seddaiu et al., 2018; Rösch et al., 2019). This is explained by the abundance of microhabitats provided by old trees, which are rare or absent in production forests (Hartel et al., 2018), but preferred by many organisms, such as saproxylic insects and their consumers (Sebek et al., 2016). From a human perspective, wood-pastures can be characterized by a high diversity of ecosystem services (Torralba et al., 2018). Wood-pasture trees provide shade, fruits, acorns and, in dry periods, canopy fodder for the animals, sources of renewable timber wood, and outstanding aesthetic value as a cultural ecosystem service (Wiezik et al., 2018; Hartel et al., 2020).

The mixed nature of wood-pasture landscapes is in many ways an advantage but a trap at the same time, as they are stuck in the “no man’s land” between agriculture and forestry, hence lacking proper policy recognition (Sandberg and Jakobsson, 2018). As a result, their management, legal representation and general valuation are often inadequate (López-Sánchez et al., 2016; Hartel et al., 2018, 2020; Sandberg and Jakobsson, 2018). For example, tree cover in pastures can cause problems in issuing subsidies under the aegis of the Common Agricultural Policy of the European Union. Land users often thin or completely remove mature trees, rarely look after tree regeneration, or even abandon traditional management and turn wood-pastures into alternative land use types, either cropland or closed-canopy production forest (Bergmeier and Roellig, 2014; Roellig et al., 2018). The diversity of both the biological entities and ecosystem services, including carbon stock, can be diminished by these trends.

In this study we aimed to understand the main concern of agriculture regarding wood-pastures, i.e. the potential ecosystem disservice of trees on pasture productivity in the temperate deciduous bioclimatic region. With this, we also aim to revisit the possibilities of tree-based climate mitigation programs regarding the planting of new trees and conserving existing ones in pastureland in a way that remains acceptable or even favorable for advocates of open ecosystems.

Specifically, we (1) used a grazing exclusion approach in Central Europe to reveal the effects of stand-alone trees on herbaceous biomass production and nutritive value under their canopy, and (2) scaled up the effects on biomass production to the level of whole wood-pastures, considering overall tree coverage. Since plant-plant interactions can be confounded by a priori environmental differences, we thoroughly assessed soil conditions, including texture, humus and nitrogen content, and moisture in open pastures, under stand-alone trees and in adjacent closed canopy forests for a comprehensive interpretation.

Considering the stress-gradient hypothesis developed for the relative intensity of competition and facilitation (Bertness and Callaway 1994), we hypothesized a generally negative effect of trees on the herb layer biomass production and herbage nutritive value, as the climate of the temperate deciduous forest zone poses little stress on plant life during the growing season, compared to Mediterranean (Armas et al., 2011) and dry tropical climates (Smith et al., 2019), where facilitation often prevails. This potential negative effect may drive the undervaluation of trees in wood-pastures of the temperate deciduous forest zone, but the effects on pasture quality, the seasonal variation and the landscape level extents are difficult to predict, as studies on these aspects have so far been carried out in stressed, Mediterranean wood-pastures (e.g., Gea-Izquierdo et al., 2009; Armas et al., 2011; Seddaiu et al., 2018).

2. Material and methods

2.1. Study sites

The study was undertaken in four European wood-pastures (Fig. 1). Two of them were in Hungary near the villages of Cserépfalu (N47.9656 E20.5593) and Erdőbénye (N48.2762 E21.3197), and the other two in Romania near the villages of Mercheasa (N46.0589 E25.3689) and Bixad (N46.1199 E25.8936). The potential vegetation in all sites is temperate deciduous forest, from which the wood-pasture physiognomy was created by thinning and subsequent low-intensity pastoral land use for centuries (Bobiec et al., 2019). Trees are several hundred years old, and include one of Romania’s oldest oak tree, aging nearly 600 years (Patrut et al., 2021). The sites cover a wide elevation range, leading to different tree species and climatic conditions among the sites (Table 1). Site conditions in Erdőbénye are close to what enable the formation of forest-steppe vegetation, which is at the limit of the tolerance of temperate deciduous forests, while site conditions in the wood-pasture of Bixad is close to the transition zone towards cold coniferous forests due to the high elevation. The other two sites are representatives of the central zone of temperate deciduous forests. We opted for this diversity of wood-pastures to identify generalizable patterns of the wood-pastures of the entire temperate deciduous forest zone.

Grassland communities of the studied wood-pastures are a rich mixture of perennial grasses and forbs. Stocking rates are around 0.5–1 animal units ha^{-1} but interannual variation is high. Bixad is grazed only by cattle, while grazers also include some sheep, buffalo, horse and goat in the other three sites. Erdőbénye is a fenced wood-pasture, within which livestock range freely. Livestock in the other sites is herded by shepherds. Grazing occurs throughout the growing season. No additional fertilization, reseeding of grasses or any other intensive grassland management technique is used in any of the sites. Erdőbénye and Bixad are privately owned, Cserépfalu is managed by the local national park, and Mercheasa is commonly used by many livestock owners of the village.

2.2. Sampling design

We randomly selected ten stand-alone trees and a 4-m^2-sized plot under them in each wood-pasture along with a neighboring open grassland plot of the same size at least 30 m from the edge of the tree’s canopy. We also selected ten 4-m^2 closed canopy forest plots in the forests around the wood-pastures. From each tree, grassland and forest plot, we sampled 1 kg soil (merged from two subsamples) both from the topsoil (0–10 cm) and from a lower layer (20–30 cm) in 2019 and assessed their texture by sorting them into sand (>0.05 mm), silt (between 0.002 and 0.05 mm) and clay (<0.002 mm) fractions, and measured plant available nitrogen content and soil organic carbon in a dedicated soil laboratory (Karcag Soil Laboratory). The two layers were investigated separately as we assumed the topsoil may be more affected by the current vegetation cover (below or beyond tree canopy) but the deeper layer informs better about potential a priori soil differences, which existed before differences in vegetation patterns had been created centuries ago. We also measured soil moisture in the upper 10 cm of the soil using FieldScout TDR 350 (Spectrum® Technologies Inc.) handheld soil moisture meter. Measurements were performed after a minimum of

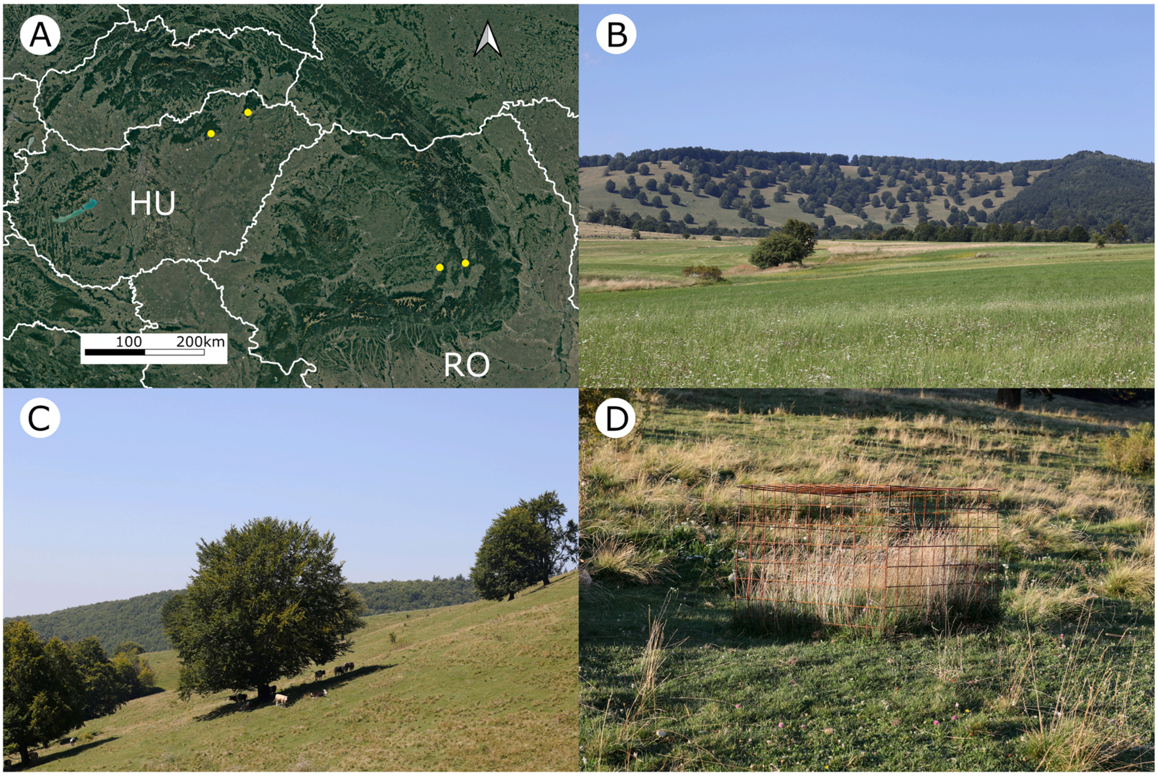

Fig. 1. Location of the studied wood-pastures in Hungary and Romania, Central Europe (A), a typical wood-pasture landscape on a hill slope near Bixad, with a closed-canopy forest on the right and a hay meadow in the foreground (B). One of the main ecosystem services of trees is improving habitat conditions for livestock by shading (C). Grazing exclusion cage near the Cserépfalu site in July, 2020 (D).

Table 1
Basic characteristics of the four studied wood-pastures.

Site	Elevation (m asl.)	Characteristic tree species	Total area (ha)
Cserépfalu (HU)	190–240	*Quercus cerris*	35.29
Erdőbénye (HU)	250–320	*Q. cerris, Q. petraea*	34.00
Mercheasa (RO)	510–660	*Q. petraea*	825.53
Bixad (RO)	790–1110	*Fagus sylvatica*	209.69

5-day-long rain free periods in the summer of 2020 and in the spring of 2021. Spring measurements in 2020 could not be performed due to Covid lockdown.

To exclude grazers, we installed a cubical steel cage with a mesh size of 10 cm × 10 cm and a volume of 1 m^3 in the wood-pasture plots (tree and grassland plots) in February, 2020 (Fig. 1D). Since there is no livestock grazing in the forests, no exclusion cages were put in the forest plots. In July, 2020, at the peak of the growing season, we collected total aboveground biomass by clipping from a 50 cm × 50 cm quadrat in the center of the exclusion cages and from adjacent grazed parts of the same plots, and also in the forest plots. We also collected biomass from non-excluded parts of every plot (tree, grassland and forest alike) the following spring in 2021, right before the start of grazing. The summer samples inform us about the potential annual plant production (ungrazed samples) and the amount consumed by the grazers (difference between ungrazed and grazed samples of each tree and grassland plot), while the spring biomass is what grows off-season without grazing and, in the case of tree and grassland plots, is available for grazers when they arrive in spring. Measurements in two seasons is also important due to high seasonal differences in plant production phenology in wooded and open landscape components, as shown e.g., by Neel and Belesky (2017) for wood-pastures in the United States.

Biomass was dried out in a drying chamber (40 °C, 5 days). To isolate potential forage biomass, leaf litter was removed, and the green biomass was retained and sorted into graminoids and forbs. We measured their weight and then homogenized them using an ordinary coffee grinder and measured the nitrogen content of the resulting powder in the Karcag Soil Laboratory. Since nitrogen content closely follows crude protein content, it is a good measure of herbage nutritive value (Collins et al., 2003).

2.3. Data analysis

All data processing and analyses were performed in R 4.2.2 (R Core Team, 2022). We visually assessed soil texture variation among landscape components (open pasture, stand-alone tree and forest) and sites using soil texture triangles prepared with the TT.plot function of the *soiltexture* package (Moeys, 2018). We also tested the association of landscape component (three levels: open grassland, stand-alone tree and forest) with soil texture using permutational multivariate ANOVA using the adonis function of the *vegan* package (Oksanen et al., 2020). We applied Euclidean distance and 999 permutations.

We prepared linear mixed-effects models with Gaussian error term for soil organic carbon, summer and spring biomass production, summer consumed biomass, as well as summer and spring plant nitrogen content using the lmer function of the *lme4* package (Bates et al., 2015). Soil nitrogen was in many cases below the detection limit (2.0 mg kg^{-1}), therefore we simplified the analysis by using binomial error term (below/above detection limit). The fixed effect was landscape component (open grassland, stand-alone tree and, where applicable, forest), and site was handled as the random effect for every mixed model. For summer soil moisture, the repeated measures design was also treated in the model. Regarding soil carbon and nitrogen content, we modeled layers separately and, for biomass, we prepared separate models for the total, graminoid and forb data. The significance of the effect of landscape component was assessed with the Anova function of the *car* package (Fox and Weisberg, 2019). If the effect of landscape component was significant, we proceeded with pairwise comparisons of landscape components, using the emmeans function of the *emmeans* package (Lenth, 2021). We also provided Cohen's d, i.e. a commonly used measure of effect size, to ensure the consistency of the pairwise differences in all sites. In most applications, $|d|$ scores below 0.2, between 0.2 and 0.8, and above 0.8 indicate small, medium and large effect sizes, respectively (Cohen, 2013). We used the lme.dscore function of the *EMAtools* package (Kleiman, 2021) for the calculations.

Finally, we scaled up the effects of trees on herb layer production to the entire wood-pastures by calculating how the overall productivity would change without trees. First, we prepared maps of each wood-pasture depicting mature trees embedded in the open grassland, and calculated the proportion of tree and grassland cover using QGIS 3.16 software. After this we used the biomass data of grassland and tree plots for extrapolation: Using the proportions of tree and grassland cover scores, we calculated the average biomass production per area unit (1 m^2) of the wood-pastures, then re-calculated how much it would be without trees, that is, only using the grassland plots of the plot pairs for scaling up to the total area of the wood-pastures. The difference between the actual wood-pasture and the hypothetical non-wooded pasture productivities were expressed in percent.

3. Results

Depending on site identity, soils ranged from sandy loam, via silty loam to silty clayey loam (Fig. 2), but according to the permutational multivariate ANOVA, neither landscape component (F=0.44, R^2 =0.008, p = 0.700) nor depth (F=1.83, R^2 =0.016, p = 0.154) affected the texture of the soils in the studied wood-pasture landscapes significantly.

Soil carbon content was uniform among the landscape components both in the top 10 cm layer (Chi^2 =2.22, p = 0.330; Fig. 3A) and at 20–30 cm (Chi^2 =1.65, p = 0.439; Fig. 3B). In contrast, plant available nitrogen content differed among landscape components in both layers (Chi^2 =8.55, p = 0.014 at 0–10 cm and Chi^2 =7.05, p = 0.029 at 20–30 cm; Fig. 3C-D). In the top 10 cm, soils of stand-alone trees contained more nitrogen than the open grassland (Cohen's d=0.94) and forests (d=1.06), which in turn did not differ from each other. At 20–30 cm, stand-alone trees still had higher amounts of nitrogen than closed canopy forests (d=0.83), but open grassland was intermediate

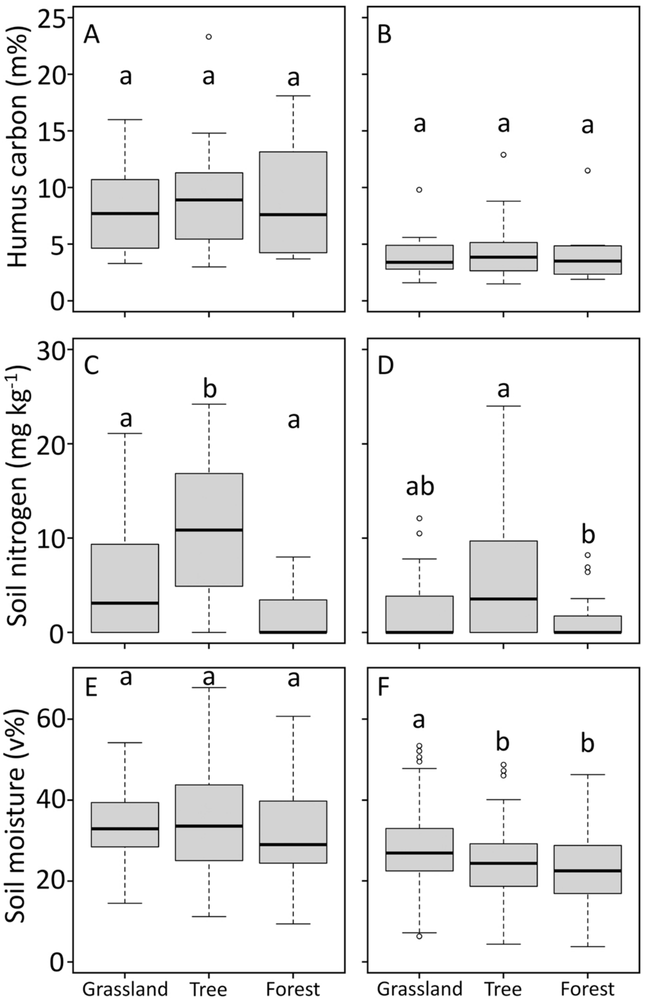

Fig. 3. Soil carbon and plant available nitrogen content in the upper 0–10 cm layer (A and C) and below at 20–30 cm (B and D), and soil moisture content in the upper 0–10 cm layer in spring (E) and summer (F) in the studied habitats. Different lowercase letters identify significantly differences groups ($p < 0.05$).

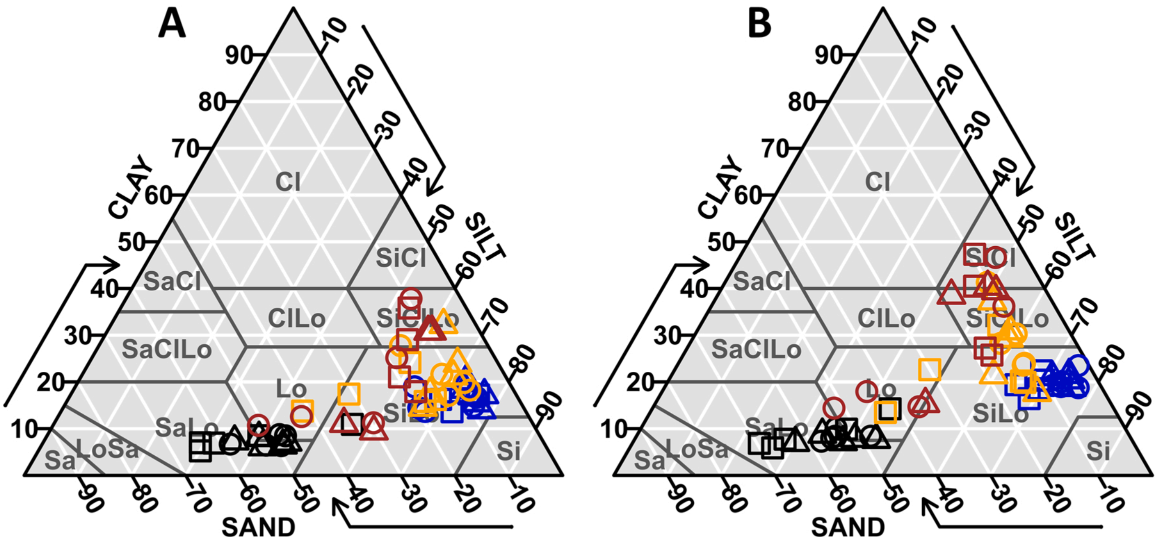

Fig. 2. Texture of the topsoil (0–10 cm; A) and deeper layers (20–30 cm; B) in Central European wood-pasture landscapes. Triangle: open grassland, circle: stand-alone trees, square: adjacent closed-canopy forest; black: Bixad, blue: Cserépfalu, red: Mercheasa, golden: Erdőbénye. Split zones in the plot space correspond to USDA soil texture classification categories; Sa: sand, Si: silt, Lo: loam, Cl: clay.

between them (Table A1). Soil moisture in spring did not differ among open grassland, stand-alone trees and forest parts of the wood-pasture landscapes (Chi^2 =3.10, $p = 0.212$), but we found differences in summer (Chi^2 =26.51, $p < 0.001$). The soil of open grassland was moister than that of stand-alone trees (d=0.37) and adjacent forests (d=0.56) (Fig. 3E-F, Table A1).

In spring, the amount of biomass differed significantly among landscape components for total values as well as for the two functional groups, graminoids and forbs (Chi^2 >38.82, $p < 0.001$; Fig. 4A-C, Table A1). Grasslands had higher total herbaceous biomass than stand-alone trees, while the forests had the lowest values. The same order was detected for graminoid biomass, while forb biomass was similarly low under stand-alone trees and in the forests, compared to open grassland. Cohen's d scores were between 0.71 and 2.57 in the significantly different group pairs. In summer, aboveground biomass was more than two times higher than in spring, but followed a very similar pattern as in spring (Chi^2 >77.67, $p < 0.001$; Fig. 4D-F; Table A1), except that graminoids did not differ between open grassland and stand-alone trees. Cohen's d scores were between 1.25 and 2.80 in the significantly different group pairs.

In spring, the nutritive value of biomass as indicated by its nitrogen content was higher under the trees than in open grassland (Chi^2 =3.96, $p = 0.047$; d=0.65; Fig. 5A), while the difference was the opposite in summer (Chi^2 =6.41, $p = 0.011$; d=0.58; Fig. 5B). Consumed biomass (i.e. removed by grazers and not replaced by growing plants) was higher in the grassland than under the trees (Ch^2 =7.18, $p = 0.007$; d=0.62; Fig. 5C).

Mapping mature trees revealed that the proportion of tree cover averaged 6.32% for the studied wood-pastures (Fig. S1, Table 2). This, considering the average spring production in open grassland (146.8 g m^{-2}) and under stand-alone trees (94.5 g m^{-2}), led to an overall 2.56% lower herbage productivity than it would have been without trees. Using the average summer herb layer biomass values in the open grassland (447.5 g m^{-2}) and under the trees (252.8 g m^{-2}), we could estimate a 2.73% lower summer herb layer biomass production in the wood-pastures than in the hypothetical treeless state. Considering the average consumed herbage in open grassland (244.0 g m^{-2}) and under the trees (156.5 g m-2), wood-pastures appear to have an average 2.25% lower overall consumed herbage amount than treeless pastures would have.

4. Discussion

In this study we aimed to look beyond the well-documented ecosystem services of trees in silvo-pastoral systems and scrutinized potential disservices to understand the unfavorable attitude of land users and decision makers towards trees. To this end, we assessed the effects of scattered wood-pasture trees on the herb layer productivity and nutritive value for grazing livestock in the temperate deciduous forest belt. We used grazing exclusion to separate the effects of grazers and trees, and also scrutinized soil conditions to reveal whether the herb layer patterns are driven by the trees or also affected by a priori site conditions. Finally, we also made an upscaling of the effects of trees to entire wood-pastures to understand the overall importance of trees for livestock production.

Our results on soil texture indicated that all three landscape components, namely open grassland, stand-alone trees and adjacent forests grow in similar basic conditions, which is in line with the origin of the wood-pastures, as they were created from continuous woodlands by thinning and introducing livestock grazing centuries ago (Bergmeier et al., 2010; Bobiec et al., 2019). The extent of tree canopy cover preceding this human intervention is a matter of debate. The closed-canopy physiognomy of present-day production forests may not be identical to prehistoric woodland conditions, which were probably kept partially open by wild megaherbivores and occasional fires (Rösch et al., 2019; Erdős et al., 2022). Nevertheless, it seems there are no notable a priori differences in soil conditions among the landscape components. Interestingly, soil organic matter content was also uniform among the landscape components, although some studies reported higher carbon stocks under stand-alone trees of wood-pastures (e.g. Seddaiu et al., 2018). However, these studies were mostly done in Mediterranean climate, where open grassland vegetation is dominated by annuals, which invest less into root systems and have fast-decaying aboveground structures, and thus contribute little to soil organic matter content. In contrast, grasslands of the temperate deciduous forest zone are dominated by perennial grasses and forbs (Habel et al., 2013), and thus the resulting

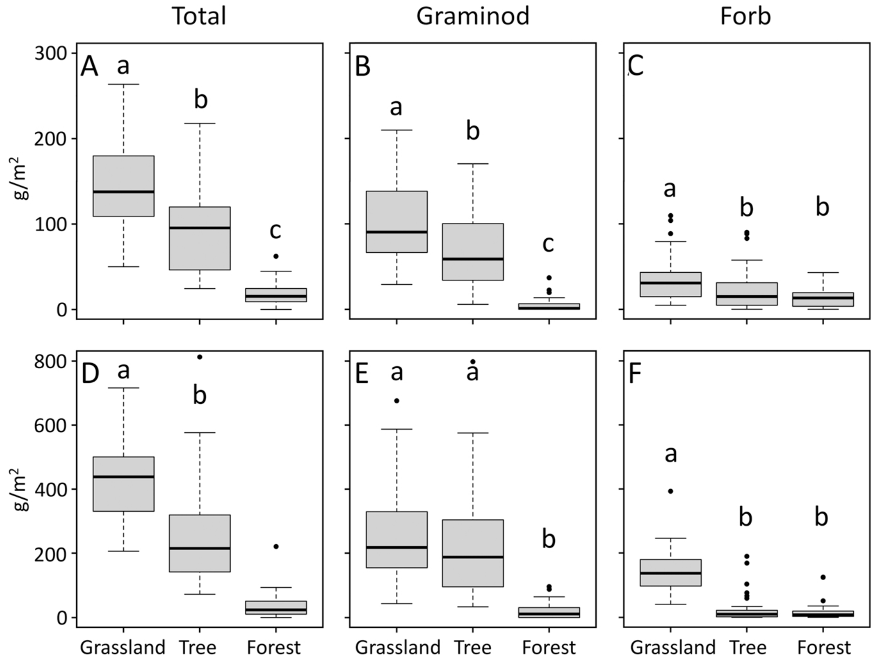

Fig. 4. Total, graminoid and forb biomass in the herb layer of the studied habitats in spring (A-C) and summer (D-F). Different lowercase letters identify significantly different groups ($p < 0.05$).

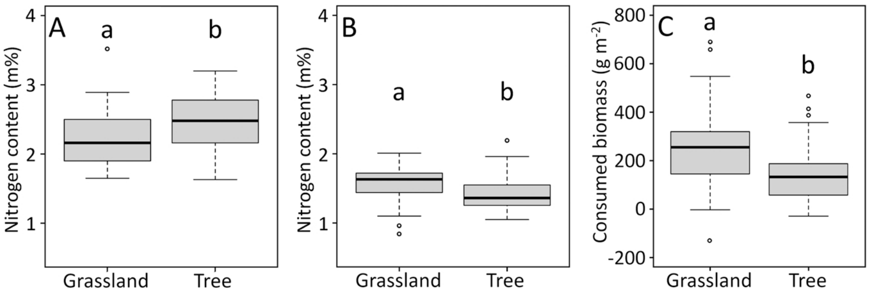

Fig. 5. Nitrogen content of the aboveground herb layer biomass in the studied habitats in spring (A) and summer (B), and the amount of consumed biomass until mid-summer (C). Different lowercase letters identify significantly different groups ($p < 0.05$).

Table 2
Results of the mapping of stand-alone mature trees (and small clumps of them) in the studied wood-pastures.

	Cserépfalu	Erdőbénye	Mercheasa	Bixad
Number	109	85	1237	346
Canopy area (mean±SD, m^2)	200 ± 211	331 ± 377	350 ± 356	335 ± 593
Overall tree cover (%)	6.17	8.29	5.26	5.54

soil organic matter content can catch up with that of stand-alone trees and forests.

Plant available soil nitrogen content, on the other hand, was clearly increased under stand-alone trees in both soil layers, but this was not a legacy from the former forest state, as forests had as low nitrogen contents as open grassland in both layers. Nutrient accumulation under wood-pasture trees is a well-known phenomenon, and explained by at least three independent mechanisms with cumulative effects. Tree canopies act as filters of airborne dust particles, containing nitrogen forms, and rain washes them down below the canopy (Bortolazzi et al., 2021). Tree roots often extend horizontally beyond the circumference of the canopy, from where they absorb nutrients, but return them to the soil under the canopy by decaying leaf litter and other dead tissues (Facelli and Brock, 2000). Finally, and probably most importantly, the shade of trees attracts grazers (see also Fig. 1C), leading to a higher density of excretes under the canopy than beyond.

High soil organic matter content ensures a good water holding capacity of soils (Lal, 2020). In line with this, soil moisture contents were relatively high, especially in spring, despite the measurements having been performed in rain free periods. In spring, at the very beginning of the active period of the deciduous canopy, all three landscape components had similar moisture relations, but in summer, when leaves had been unfolded for months, canopy interception and transpiration decreased the moisture content of the soil. As a result, both stand-alone trees and forests had drier soils than open grassland, despite the shading of the canopy, which reduces evaporation from the soil surface. Such a moisture pattern is known from natural temperate forest-grassland mosaics and also from gap cutting experiments in temperate deciduous forests (Tölgyesi et al., 2020; Kovács et al., 2020).

Biomass production and nutritive value relations are determined by the effects of trees on the sub-canopy environmental conditions. In spring, when shading was low due to the dormancy of trees and soil moisture was available in abundance, the herb layer could take advantage of the elevated nitrogen content in the soil and had a better nutrient value than open grassland. However, biomass production remained below that of open grassland, which we explain with the distinct species composition of the two landscape components (Rolo et al., 2015; López-Sánchez et al., 2016). Most species under the trees are not spring annuals in our bioclimatic zone but perennial species (Tölgyesi et al., 2018), therefore those species were filtered from the regional species pool that can cope with the shady and dry summer conditions, which probably enables lower overall growth rates, constraining spring biomass production. However, these details need further studies to confirm, for example, with transplantation experiments (see e.g. Gavazov et al., 2014). Nevertheless, biomass production under stand-alone trees were still much higher than in the forest.

In summer, when trees reduced light and moisture availability compared to the open grassland, biomass production was hampered, and the high soil nitrogen content could not be utilized either, as plant nitrogen content dropped below that of open grassland herbage. This latter effect can be attributed to a decrease of forb biomass and the lack of change in graminoid biomass, as forbs have been shown to have higher protein content than grasses in temperate wood-pastures (Hernandez-Esteban et al., 2019). The differential reaction of forbs and grasses to the effects of trees is explained by the relatively lower competitive ability of forbs (Segre et al., 2014; Erkovan et al., 2022), so the additional competition with trees for moisture and light resulted in the suppression of forbs, and an eventual reduction in consumed biomass.

Overall, the findings on biomass suggest that the overstorey-understorey interaction starts with a mixture of facilitative and competitive outcomes in spring, which shifts in summer into a clear competitive suppression of the herb layer. Although there may be some inter-annual variation of these relations, they seem to be in contrast with many Mediterranean and dry tropical situations, where the effect of shading and soil nutrient enrichment and thus the reduction of stress prevails and often adds up to net facilitation (e.g. Gea-Izquierdo et al., 2009; Seddaiu et al., 2018; Smith et al., 2019). Our hypothesis, the overall negative effects of trees on herb layer biomass production, which can be viewed as a potential ecosystem disservice, is confirmed. This may explain the negative attitude of land users and decision makers towards trees when the wood-pastures are considered solely as herbage producing systems. The partly opposing pattern in spring and summer, however, lessens this ecosystem disservice and calls attention to a diversified forage supply in spring, with lower abundance but better nutritive value under the trees. Furthermore, when we estimated the overall effect of the trees on herbage production considering current tree cover proportions, we revealed that the loss of herbage amount in the study year was less than 3%, which seems negligible both ecologically and economically. In addition, the importance of this herbage loss is completely offset by the positive effects of shading on the well-being and productivity of the livestock. Providing shade for animals in pastures leads to less aggressive behavior, lower body temperatures and lower respiration rate (Schütz et al., 2010). According to shade addition experiments, these physiological effects can lead to a 3% increase in the milk production of dairy cattle after 10 days (Fisher et al., 2008), and the figures can rise above 10% if shade is available in the pastures throughout the warm months (Valtorta et al., 1996).

In summary, wood-pasture trees in the temperate deciduous forest zone are mostly competitors of herb layer vegetation, but the overall effect on wood-pasture productivity seems very low. Wood-pastures with higher forest cover, or wood-pastures on north-facing slopes, where the shading effect of trees is more pronounced, may experience a larger impact on herbage production. Nevertheless, in traditional wood-pasture landscapes, such as our sites, the negative valuation of trees by policy makers and land holders is not justified, and the positive direct effects of trees, most importantly shading, offset the consequences of the unfavorable overstorey-understorey interaction for livestock husbandry.

Our results suggest two parallel courses of actions. First, existing stand-alone trees should be preserved, with their centuries-old, massive carbon stock and the many microhabitats and additional ecosystem services they provide. This suggestion is in line with many other wood-pasture studies that stress the importance of tree conservation (e.g. Plieninger et al., 2015; Sebek et al., 2016; Hartel et al., 2018), the only difference being that they mostly focused on the positive effects of trees and ignored potential disservices that may drive some stakeholders, whereas we quantified these and could reject their importance. Second, as tree regeneration is inadequate in most European wood-pastures (Plieninger, 2007; Smit and Ruifrok, 2011), a greater attention should be paid to protecting seedlings from browsing and trampling, e.g. by allowing patchy shrub encroachment, where shrubs can protect saplings during their early ontogenesis (Varga et al., 2015). Furthermore, advocates of open ecosystems look at tree planting in ancient pasture grasslands as a taboo, and a potential threat to their biodiversity and ecosystem services (Feurdean et al., 2018; Veldman et al., 2019). Full afforestation should obviously be avoided, but establishing scattered trees in the grassland matrix with eventual tree cover proportions comparable to those of existing wood-pastures is highly advisable, or should even be handled as the new standard. Open grasslands in Europe still cover nearly 1 million km^2 (Dengler et al., 2020), while wood-pastures have shrunk to 20% of this in area (Plieninger et al., 2015); thus, there is realistic opportunity to implement our recommendation. Scattered tree planting with native species will lead to higher overall biodiversity, a wider array of ecosystem services (including increased carbon capture and storage), potential microclimatic refuges for grassland fauna under ongoing climate change (see also Thakur et al., 2020), some seasonal diversification of herbage nutritive value, and no notable fallback in forage production or livestock yield in the temperate deciduous forest zone.

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CRediT authorship contribution statement

Csaba Tölgyesi: conceptualization, data curation and analysis, funding acquisition, data collection, visualization, writing (draft); András Kelemen: data collection, writing (review & editing), Zoltán Bátori, Réka Kiss, Alida Anna Hábenczyus, Krisztina Havadtői, Anna Varga, László Erdős, Benedek Tóth, Kata Frei: data collection, writing (review & editing); Péter Török: conceptualization, funding acquisition, writing (review & editing).

Data Availability

Data will be made available on request. Data will be archived in Dryad Data Repository upon the acceptance of the 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.2023.108477.

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