Agroforest Syst (2025) 99:272
https://doi.org/10.1007/s10457-025-01373-8

The potential of agroforestry and small fields to enhance ground-dwelling spiders

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Received: 28 May 2025 / Accepted: 13 October 2025

Abstract Agroforestry systems integrate open and woody elements within agricultural landscapes, creating structurally complex ecosystems that provide habitats for diverse taxa, including spiders. This study examined the effect of agroforestry systems on ground-dwelling spiders across multiple European countries. In each country, several mature agroforestry plots were compared with non-agroforestry agricultural and woody reference plots. Our findings reveal that agroforestry supports species from both open and forested habitats, contributing to landscape-scale biodiversity. Alpha diversity was higher in silvopastures than in forests, but beta diversity (turnover) was not significantly different between agroforestry and other habitat types. Instead, there was a trend towards decreasing spider richness with increasing field size, across all habitat types. High

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Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10457-025-01373-8.

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variability in spider diversity across regions suggests that local environmental factors, such as tree species, management practices, and climate, play a key role in shaping spider communities. Our study supports that mosaic of small fields with diverse land uses, combined with seminatural habitats and structurally heterogeneous productive systems like agroforestry, can enhance biodiversity and species-rich agricultural landscapes.

Keywords Agroforestry · Community composition · Silvoarable systems · Silvopastoral systems · Spiders · α-diversity · β-diversity

Introduction

Agroforestry systems, which deliberately integrate trees with agricultural crops and/or pastures, have the potential to reconcile food production with biodiversity conservation and broader environmental benefits (Pantera et al. 2021; Smith et al. 2013). The advantages of agroforestry, based on the synergies between trees and crops or pastures, are both economic and environmental (Palma et al. 2007a; Kay et al. 2019a). Agroforestry systems improve carbon storage, soil fertility, water quality, and nutrient cycling while mitigating the risk of soil erosion (Malézieux et al. 2009; Mosquera-Losada and Prabhu 2019; Palma et al. 2007b; Pardon et al. 2017; Smith et al. 2013; Torralba et al 2016). Furthermore, agroforestry systems, due to their structural heterogeneity, provide valuable habitats for taxa such as birds (Edo et al. 2024; Hartel et al. 2014; Gibbs et al. 2016) and bats (Edo et al. 2025). These systems have also been shown to support arthropods (Boinot et al. 2019, 2020; Pardon et al. 2019; Kay et al. 2019b; McAdam et al. 2007; Peng and Suon 1996; Bentrup et al. 2019), offering promising opportunities to mitigate the drastic global decline in their diversity and abundance observed over recent decades (Müller et al. 2024; van Klink et al. 2021; Wagner et al. 2021). A major driver of this ongoing decline of arthropods is habitat loss, primarily caused by the simplification and homogenization of agricultural systems (Benton et al. 2002 and 2003; Šálek et al. 2018).

Among arthropods, spiders are particularly sensitive to environmental changes and occur in high diversity and density across all terrestrial ecosystems (Foelix 2011; Nyffeler 2000), making them excellent bioindicators and early-warning organisms for studying shifts in the food web or habitat modifications (Marc et al. 1999; Branco and Cardoso 2020; Pearce and Venier 2006). In addition, as predators, spiders provide essential ecosystem services in agricultural landscapes, particularly through natural pest control (Michalko et al. 2019a,b; Marc et al. 1999; Nyffeler and Birkhofer 2017). Crop management practices that lead to habitat destruction and homogenization, along with forest fragmentation, have been shown to negatively impact spider communities (Birkhofer et al. 2015a, b, c; Thorbek and Bilde 2004; Prieto-Benítez and Méndez 2011). However, in some cases, spider populations may benefit from environmental changes, particularly when disturbances and management interventions enhance habitat heterogeneity. This can occur, for example, through low-intensity grazing in grasslands (Horvath et al. 2009) or the introduction of woody elements in agricultural fields. The increased structural complexity provided by trees and vegetation strips in alley cropping systems has been shown to provide valuable habitats for overwintering spiders and to support spider abundances (Boinot et al. 2019; Matevski et al. 2024). Grazing, which influences vertical stratification and enhances field heterogeneity, has also been found to benefit spider diversity and species richness in landscapes with agroforestry systems (Moreno et al. 2016; Barriga et al. 2010). Although some studies have explored the effects of one type of agroforestry system (silvoarable or silvopastoral) on spiders in a particular region, to our knowledge, no study has investigated the impact of both silvoarable (tree-crop) and silvopastoral (tree-pasture) systems on spiders at the European scale.

In this study, we investigated ground-dwelling spider diversity in agroforestry systems (silvoarable and silvopastoral systems) and control plots across five temperate and three Mediterranean regions in western Europe. We compared ground-dwelling spider communities in agroforestry systems with those found in open croplands, pastures, forests, and orchards, aiming to improve our understanding of the effects of agroforestry systems on spider communities. Furthermore, we explored to what extent spider communities were affected by agroforestry type, whether cultivated or grazed.

These findings should inform about the potential role of agroforestry in the transition toward more resilient and biodiversity-friendly agricultural systems while maintaining productivity, a key objective of modern agriculture (Tilman et al. 2011; Bommarco et al. 2013; Helfenstein et al. 2020).

We hypothesize that in agroforestry systems, where the combination of trees with cropland/pastures enhances habitat heterogeneity, ground-dwelling spider communities will comprise species from both open and wooded habitats, as well as ecotone specialists and eurytopic species. Consequently, we expect species richness (α-diversity) to be higher in agroforestry systems compared to croplands, pastures, forests, and orchards. Additionally, due to the greater vertical heterogeneity in agroforestry systems, which creates a range of microclimates at ground level, we hypothesize that β-diversity—particularly the turnover component within plots—will be higher in agroforestry systems than in other habitat types. We further hypothesize that species richness will be higher in small plots than in larger ones due to spillover and resource complementation between habitats.

Material and methods

Study sites

Ground-dwelling spiders were sampled in 22 agroforestry and 44 control plots (hereafter termed as "plots") across eight sites located in different biogeographical regions (in the following referred to as "sites") (Fig. 1). Agroforestry plots were either silvoarable (combination of trees and crops; eight plots sampled across England, Switzerland and Southern France) or silvopastoral systems (combination of trees and livestock; fourteen plots sampled across Northern Ireland, Germany, Central France, Italy and Spain). Two to three agroforestry plots were sampled in each site. In addition to each agroforestry plot, spiders were sampled in control plots that always contained the same woody or agricultural components as the corresponding agroforestry plot. These control plots were located as close as possible to their reference agroforestry plot (between 200 m and 6 km) to minimize the variation of e.g. climate, soil, and the surrounding landscape (Fig. 1). In total, 13 open pastures, 13 forests and 2 orchards were sampled as controls for the silvopastoral plots (n = 14) and 6 crop plots, 6 forests and 4 orchards were sampled as controls for the silvoarable plots (n = 8). Fruit or nut

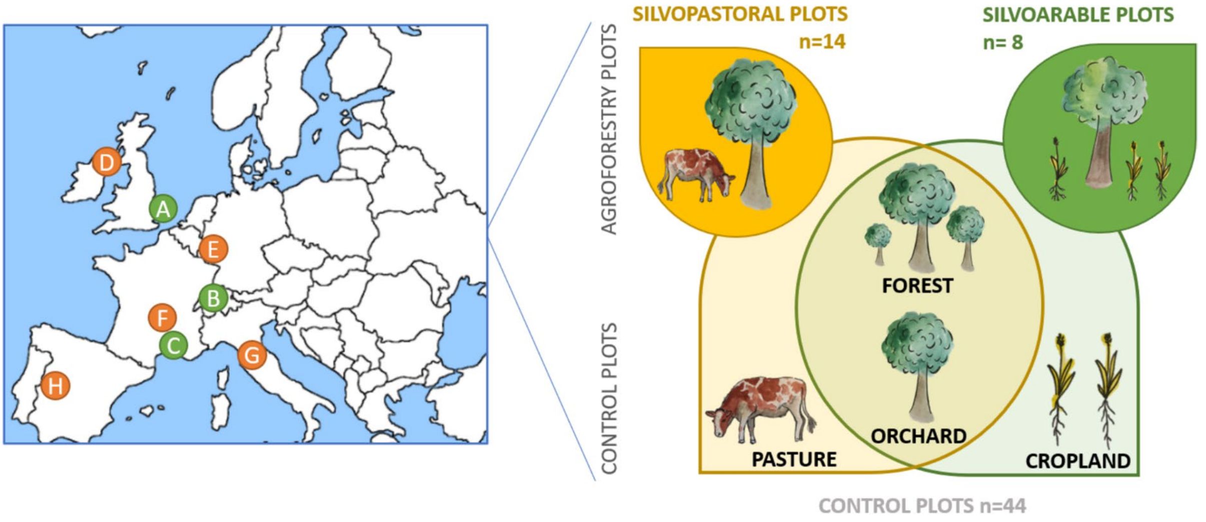

Fig. 1 Geographic location of the silvoarable (A–C) and silvopastoral (D–H) study sites. Green circles = silvoarable sites: A = Wakelyns (UK), B = Möhlin and Sursee (CH), C = Restinclières (FR) Orange circles = silvopastoral sites: D = Loughgall (UK), E = Bannmühle (DE), F = Lamartine (FR), G = Tenuta di Paganico (IT), H = Dehesa de Majadas (ES). In each site, 2–3 agroforestry (either silvopastoral or silvoarable) plots were sampled. In addition to each agroforestry plot, 2–3 control plots were sampled

orchards were sampled only if the trees of the agroforestry plots were fruit (Germany and Switzerland) or pine trees (in Southern France). We defined forests as areas with more than 10 percent tree cover over at least 0.5 ha and which contained trees aged more than 30 years, but excluding trees of agricultural production systems (FAO 2018). The tree species in the orchard controls were the same as those planted in the agroforestry plots. In this study, only agroforestry and orchard plots with mature trees planted at least 12 years prior to the year of sampling were studied. Information on plot management, tree species, age and density as well as crops or livestock associated to each plot can be found in Supporting Table S1. Plot size was measured using Google Earth (2025) (https://www.google.com/earth). On average, plot size was 2.51 ± 0.64 hectares (ha ± SE) for silvoarable plots, 9.3 ± 5.01 ha for silvopastoral plots, 22.3 ± 6.89 ha for forests, 0.9 ± 0.21 ha for orchards, 9.5 ± 6.68 ha for croplands, and 5.7 ± 1.91 ha for pastures (sizes for each sampled plot are given in Supporting Table S1).

Spider sampling and identification

Ground-dwelling spiders were sampled using pitfall traps during three different sampling periods in spring, when the spider activity-density is the highest (Cardoso et al. 2007). In England, Northern Ireland, Central France, Switzerland and Germany the sampling took place in April, May and June 2021 while in Southern France, Italy and Spain it took place in March, April and May 2022. We aimed to sample the ground dwelling (epigeal) spider communities and compare them between habitats (silvoarable and silvopastoral systems, forests, croplands, pastures and orchards), being aware that higher vegetation strata, or tree canopies are not sampled. Pitfall traps are highly effective in catching large numbers of species with minimal effort (Curtis 1980). In each plot, four pitfall traps (depth: 9.5 cm, diameter: 6.8 cm) were positioned equidistantly (6.6 m from each other) along a 20 m transect, at least 20 m away from the habitat edge. In wooded plots (forests, orchards and agroforestry systems) the traps were positioned to cover both open and shaded areas, with the second trap always placed under a tree (1 m away from the tree trunk). In plots with trees planted in rows, the fourth trap was always placed in the middle of the crop/pasture row. The angle between the transect and the tree rows was varied to ensure the 20 m transect length between the center of the alley and the tree line (Fig. 2). Pitfall traps were filled with 100 ml of a 1:2 mixture of propylene glycol and tapwater, with odor-free detergent added to break the surface tension and a bittering agent to prevent disturbance by large mammals (e.g. wild boar, deer). Traps were exposed for 10 days in each plot and this procedure was repeated for the three sampling periods, resulting in a total of 30 sampling days per plot and a total of 264 pitfall traps placed across the 66 sampled plots. After 10 days, pitfall traps were emptied and the captured arthropods were stored in ethanol (80% vol.). Adult spiders were identified to species level and immature spiders to family level using reference identification keys and European databases: Roberts (1996), Nentwig et al. (2010), Oger (2015), World Spider Catalog (2025), Muséum national d'Histoire naturelle & Office

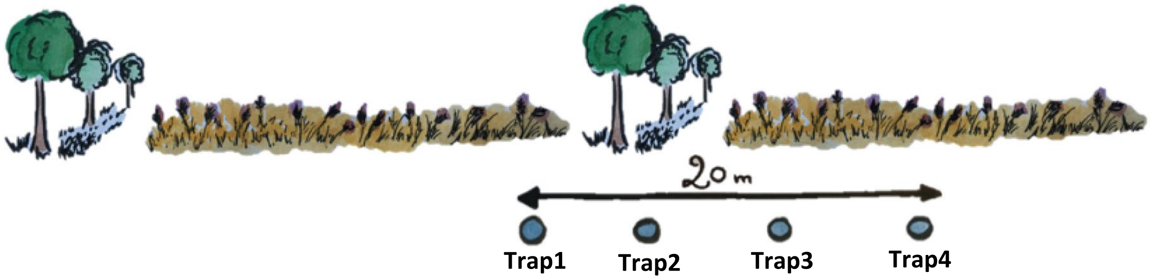

Fig. 2 Equidistant placement of the pitfall traps on the 20 m transect. In plots with trees, trap 2 was always placed under a tree (1 m from the tree trunk) and trap 4 in the middle of the crop or pasture alley. Traps 1 and 3 are placed in the crop or pasture alley

français de la biodiversité (2003–2025), Arachnologische Gesellschaft e.V. (2025). The nomenclature follows the World Spider Catalogue (2025). The identifications of rare or cryptic species were confirmed by expert arachnologists (see Acknowledgements). Two potentially undescribed species (total of three individuals) could only be identified at genus level and were thus treated as morphospecies in this study. If females could not be identified at species level, the number of females was set proportionally to the number of males present in each site (2 females of *Pardosa lugubris/saltans* in Switzerland and 7 females of *Pardosa proxima/tenuipes* in Southern France and Switzerland).

Data analysis

Prior to the analysis of community composition (RDA), species richness and α-diversity, the results of the three sampling periods were summed per pitfall trap and per plot (sum of the identified spiders of 12 traps per plot for each of the 66 different plots).

To assess the influence of different habitats types on spider community composition, we applied constrained ordination. A partial redundancy analysis (pRDA) was performed based on the number of sampled individuals per species and per plot over the season, with land-use type (hereafter "Habitat") as explanatory variable and site as conditional variable (R package vegan, function rda, Oksanen et al. 2013). Only species that occurred on more than two plots were retained in the analysis. Prior to analysis, the community data matrices were Hellinger-transformed, to reduce the impact of dominant species and meet the assumptions of linear ordination methods (Legendre and Gallagher 2001). The significance of the pRDA model was assessed using a permutation test with 9999 permutations (R package vegan, function permutest, Oksanen et al. 2013).

To assess the effect of habitat on α-diversity, species richness and inverse-Simpson indices (hereafter termed as "Simpson diversity") (Simpson 1943) were computed for each plot, using the PAST software (Hammer 2001) (see Supplementary Table S1). Linear mixed-effect models were fitted (R package lme4, function lmer, Bates et al. 2015b, a) with habitat type set as explanatory variable and "site" as a random factor, due to the nested design of the study (equations: lmer (SpR ~ Habitat + (1|Site) and lmer (Inv-Simpson ~ Habitat + (1|Site)). An Anova was conducted to evaluate the significance of the fixed effect, and post-hoc tests were used to determine the pairwise differences between habitats (R package emmeans, function emmeans, Lenth 2022). To determine the effect of plot size on species richness, linear mixed-effect models with the log transformed plot size as explanatory variable and "site" as random factor were fitted (equations: lmer (SpR ~ log(Size) + Habitat + (1|Site)). An Anova was conducted to evaluate the significance of the fixed effect. Due to damage by wildlife, 25 out of 792 trap catches were missing (see in Supplementary Table S1 the total number of traps collected per plot). To make sure that the missing traps did not affect our results, we fitted a model with Habitat and Number of available samples as explanatory variables (equations: lmer (SpR ~ Habitat + Number of traps + (1|Site). As the results were highly similar, we show the results without accounting for missing traps.

To assess differences in β-diversity between habitats, we performed pairwise comparisons of spider community composition using the Jaccard dissimilarity index at two different levels: (a) pairwise comparison of the spider communities between plots within a same habitat in each site (identified spiders were summed per plot over the three samplings, pairwise comparison of 66 plots in total) (b) pairwise comparison of the communities between traps of a same plot, within habitat and within site (identified spiders were summed over the three samplings for each trap, pairwise comparison of 264 traps in total). For each pairwise comparison, ß-diversity ($\bumpeq_{jac}$ total Jaccard dissimilarity) was partitioned into two components: the turnover ($\bumpeq_{jtu}$ species replacement) and nestedness ($\bumpeq_{jne}$ species loss or gain due to differences in species richness) (R package betapart, function beta.pair, Baselga 2010). The objective of this analysis was to determine the spider species turnover, independent of richness differences. Moreover, the nestedness component did not contribute significantly to β-diversity patterns. For these reasons, we show only the results of the turnover component here. For both analyses (a) and (b), we calculated the mean values of turnover across habitat and generated a boxplot to visualize the distribution of this β-diversity component. To assess the effects of country and habitat type on β-diversity, we conducted an analysis of variance (Anova) (aov

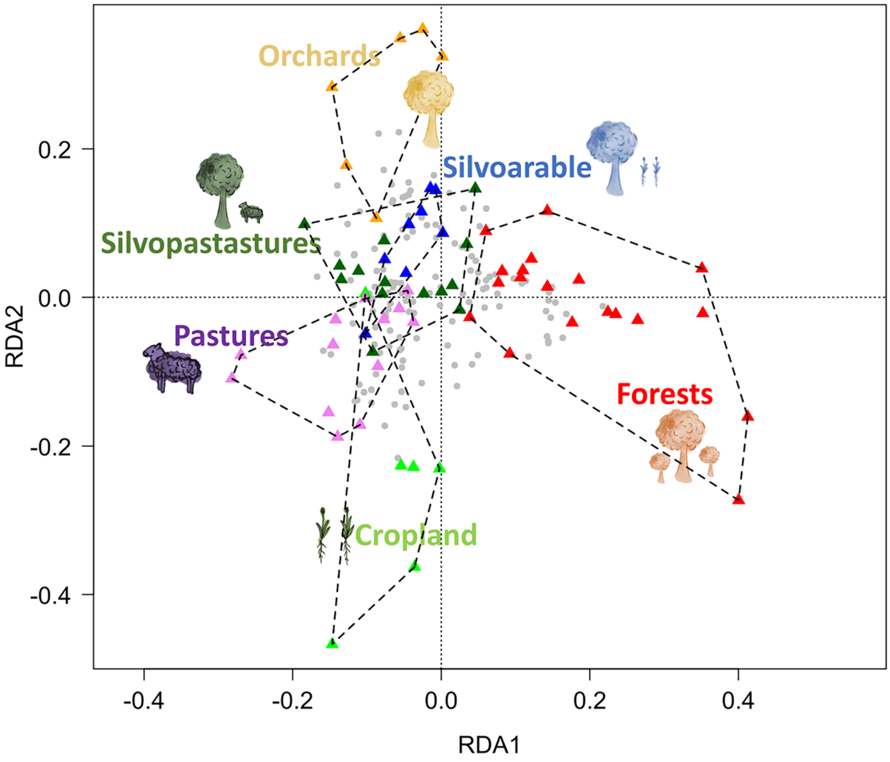

Fig. 3 Composition of the spider communities in the different habitat types (silvopastures, pastures, orchards, croplands and silvoarable systems), analysed with redundancy analysis. Grey dots indicate centroids of spider species, and dashed lines represent minimum convex polygons around habitat types with the colored triangles indicating individual sampling plots

($\Bumpeq_{tu}$, ~ Country + Habitat2) (package stats, function aov, (Chambers et al. 1992)).

Finally, we ran an indicator species analysis using the package labdsv, function indval, (Dufrêne and Legendre 1997) to assess, based on both their relative abundance and frequency within a habitat, which spider species are strongly associated with each habitat type. For the indicator species analysis, we excluded all species with <6 individuals in total, and which occurred on <5 plots. For species-level analyses (pRDA, α- and β-diversity), only adult spiders (males and females) were included. In contrast, total abundances of families described in Sect. "Spider communities and habitat" considered both adult and immature individuals, excluding only the earliest developmental stages of *Lycosidae*. For all statistical tests, p-values lower than 0.05 were considered as significant. All statistical analyses were conducted in R version 4.2.2 (R Core Team 2022).

Results

Spider communities and habitat

In total, we captured 10,100 spiders, including 8977 adult individuals, belonging to 32 different families and 308 species. The most abundant families were Lycosidae (49% of all individuals), Linyphiidae (27%), Gnaphosidae (7%), Tetragnathidae (5%) and Thomisidae (3%). According to the pRDA, spider community composition differed significantly between habitat types ($F = 1.72$, $p = 0.0001$). In the pRDA, habitats explained 9.5% of the total variance after controlling for country effect (explaining 31.8% of the variance). Agroforestry systems occupied an intermediate position in ordination space, showing partial overlap with croplands, pastures, orchards and forests (Fig. 3). The RDA also highlights that silvopastures showed a higher dispersion and thus a more variable species composition than silvoarable systems.

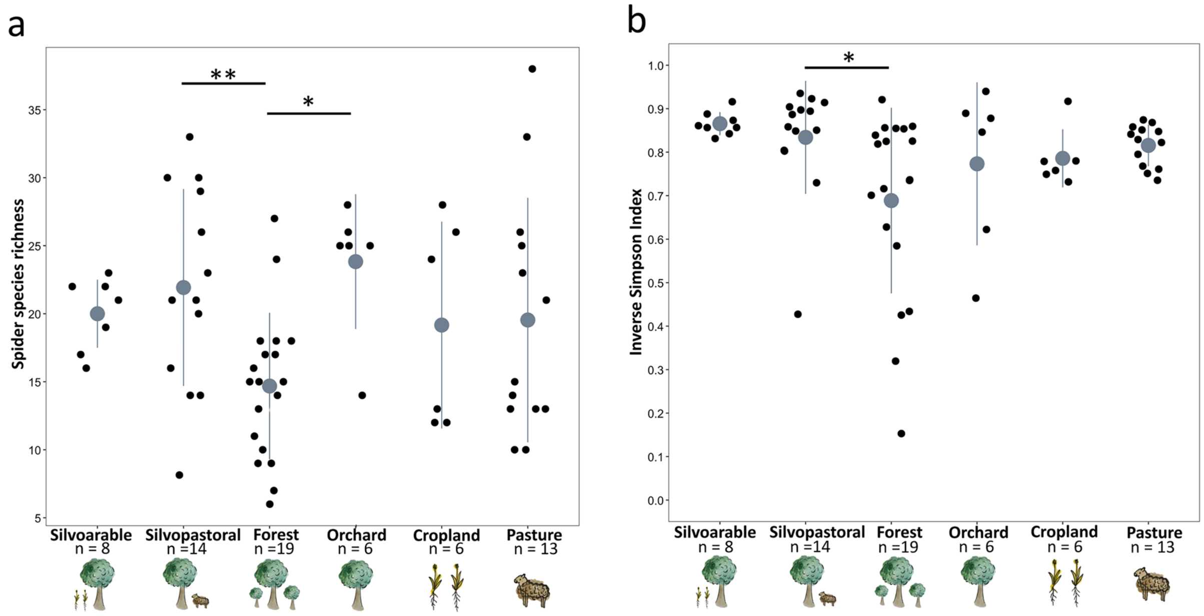

Fig. 4 **a** Spider species richness (mean) **b** Inverse Simpson index (mean) (referred as Simpson diversity) per habitat type and with deviation error bars (in grey). Significance levels: $*p<0.05$, $0.001<**p<0.01$. See Supplementary Table S4 for the detailed results of species richness and Simpson diversity in the different habitats as well as mixed-effect models and post hoc tests used to determine the pairwise differences between habitats

α-diversity

The most abundant species were *Pardosa palustris* (916 individuals), *Pardosa saltans* (848 ind.), *Erigone dentipalpis* (682 ind.), *Pardosa amentata* (540 ind.), *Pardosa pullata* (478 ind.), *Pardosa prativaga* (454 ind.), *Pachygnatha degeeri* (403 ind.), *Alopecosa pulverulenta* (392 ind.), *Erigone atra* (372 ind.) and *Tenuiphantes tenuis* (240 ind.). Habitat type had a strong influence on spider species richness ($F=5.56$, $p<0.001$). Species richness was 49% higher in silvopastoral systems ($p=0.02$) and 62% higher in orchards ($p=0.012$) compared to forests (Fig. 4a, Supplementary Table S4a). Simpson diversity differed significantly between habitats ($F=3.25$, $p=0.013$) and was significantly higher in silvopastoral systems compared to forests ($p=0.032$) (Fig. 4b, Supplementary Table S4b). There were no significant differences in species richness and Simpson diversity between the other habitats. Spider abundance showed no significant differences between the different habitat types (Supplementary Figure S2 and Supplementary Table S3). Spider species richness decreased marginally significantly with increasing plot size ($F=3.72$, $p=0.0586$, Fig. 5), due to shared variance with the habitat. Effects of plot size on spider abundance ($F=0.401$, $p=0.529$) and Simpson diversity ($F=0.11$, $p=0.743$) were not significant.

β-diversity (turnover)

Species turnover between plots ($\Bumpeq_{jtu}$) differed significantly between countries ($F=3.62$, $p=0.019$). However, there were no significant differences in between-plot species turnover among habitat types ($F=1.85$; $p=0.169$). Although not significant, turnover was the highest in forests and orchards and the lowest in silvoarable systems and pastures (Fig. 6a). Similarly, species turnover between traps of the same plot differed significantly between countries ($F=5.1$; $p= <0.001$) but not between habitat types ($F=1.15$; $p=0.347$) (Fig. 6b). Here, turnover was the highest in forests and the lowest in silvoarable and croplands (Fig. 6b).

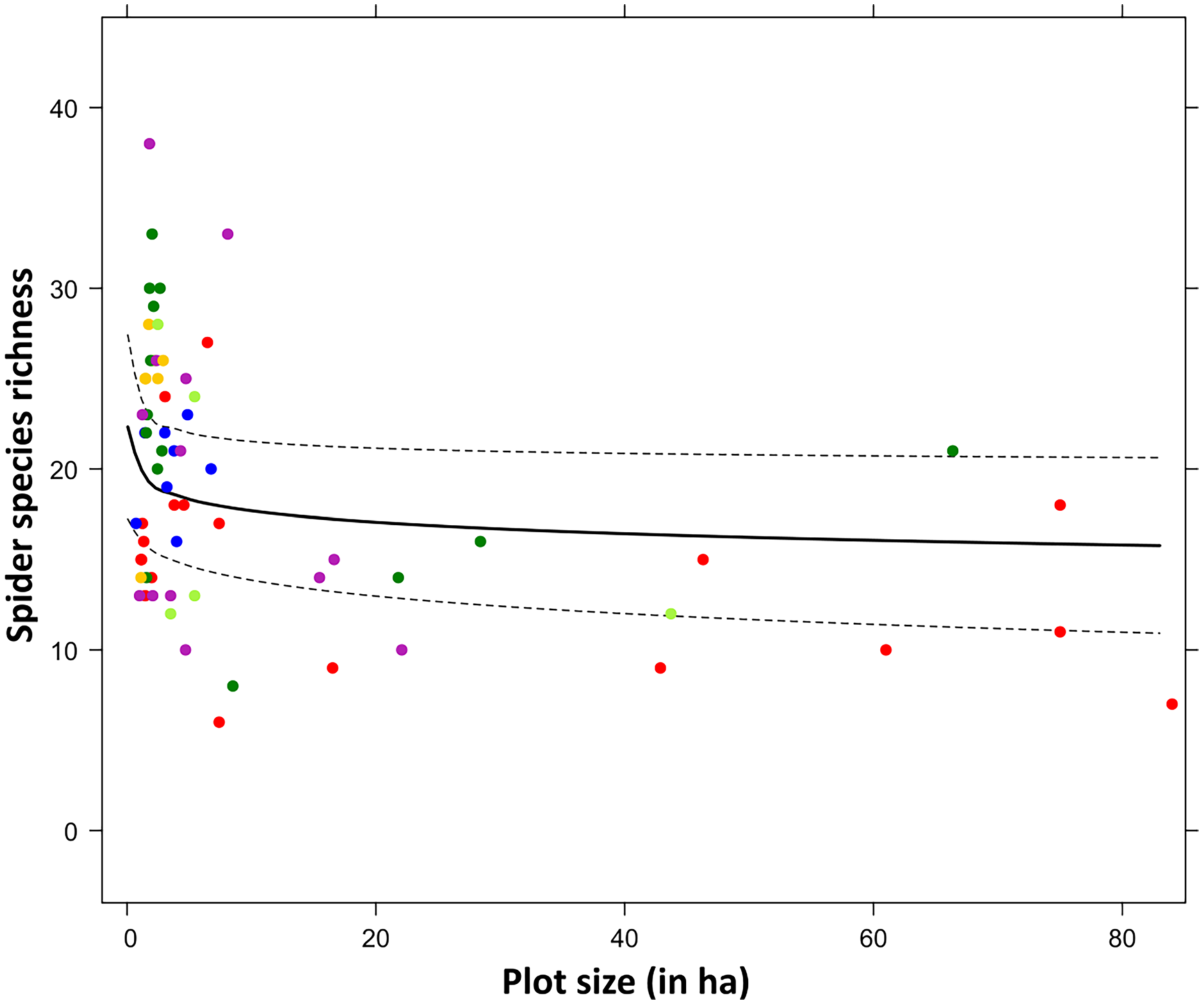

Fig. 5 Effect of plot size in hectares (ha) on spider species richness across habitat types: silvoarable (dark blue dots) and silvopastoral (dark green dots) agroforestry systems, forests (red dots), orchards (yellow dots), cropland (light green dots) and pastures (purple dots). (Color figure online)

Indicator species

The indicator species analysis showed a strong association of the two species *Trochosa ruricola* and *Diplostyla concolor* with silvoarable plots (Table 1). By contrast, no indicator species were found for silvopastures. Four species were associated with open agricultural land: *Pardosa proxima*, *Diplocephalus graecus* and *Oedothorax apicatus* were associated with croplands and *Argenna subnigra* was associated with pastures. *Pardosa saltans* was a significant indicator of forests while *Ozyptila simplex, Hahnia nava, Pardosa hortensis* and *Micrargus subaequatilis* were indicator species for orchards.

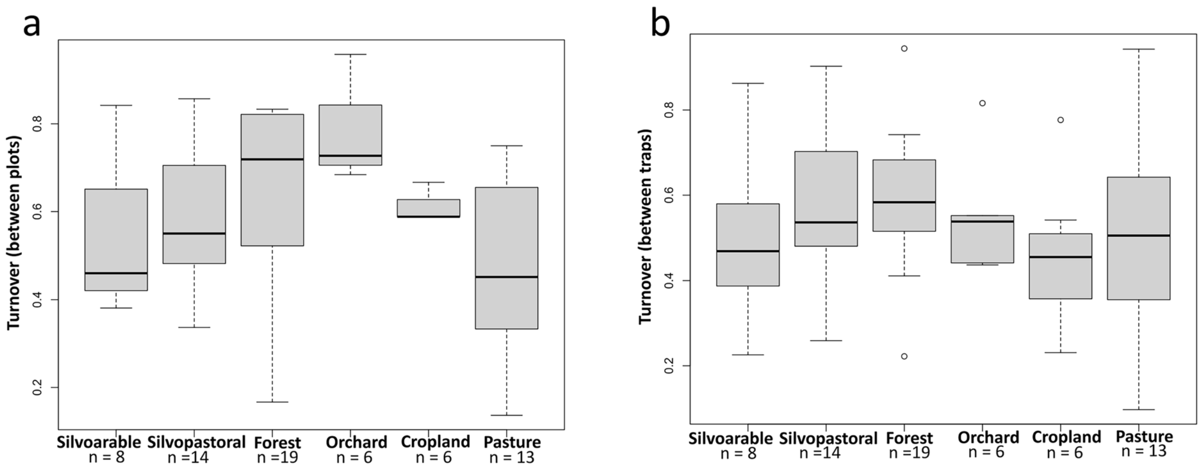

Fig. 6 Median species turnover ($\Bumpeq_{jtu}$) calculated via pairwise comparison of the spider communities **a** between plots of the same habitat type in each country **b** between traps of a same plot

Table 1 Indicator species analysis indicating species association with different habitats. Higher indicator value indicates stronger association of species with the given habitat. The last column indicates the total number of plots on which the species was found. Only p-values < 0.05 and species occurring on more than five plots are listed in the table

Species	Preferred habitat	Indicator value	P value	Number of plots
Trochosa ruricola	Silvoarable plots	0.410	0.009	22
Diplostyla concolor	Silvoarable plots	0.541	0.002	13
Pardosa_saltans	Forests	0.395	0.036	15
Ozyptila simplex	Orchards	0.263	0.044	7
Hahnia nava	Orchards	0.342	0.014	11
Pardosa hortensis	Orchards	0.344	0.014	14
Micrargus subaequalis	Orchards	0.351	0.006	7
Pardosa proxima	Croplands	0.420	0.007	5
Diplocephalus graecus	Croplands	0.428	0.003	5
Oedothorax apicatus	Croplands	0.475	0.003	6
Argenna subnigra	Pastures	0.296	0.027	5

Discussion

As hypothesized, spider communities in agroforestry systems comprised species from both open and wooded habitats, supporting a diversity of habitat preferences. Only few significant differences were observed in α-diversity between agroforestry systems and other habitat types, except that silvopastures and orchards exhibited higher alpha diversity than forests. β-diversity (turnover) between plots and between traps within plots showed no significant differences. Nevertheless, this study highlights the role of silvoarable and silvopastoral systems in supporting characteristic spider communities comprising species from different habitat types.

Spider communities

Our study demonstrated that spider community composition differed between habitats and that agroforestry systems support distinct spider assemblages comprising species from both open and wooded environments. This finding aligns with Matevski et al. (2024), who identified the coexistence of forest specialists, open-habitat specialists, and eurytopic spiders in silvoarable systems in Germany. Similarly, Hemm and Höfer (2012) reported that structurally diverse grasslands with shrubs and increased litter cover in Germany hosted forest dwellers, hygrophilous species, and openland spiders. Diaz et al. (2013) also found that Spanish silvopastoral systems (“Dehesas”) support both forest and grassland species. The presence of spider communities with diverse habitat preferences in agroforestry can be attributed to their greater structural complexity compared to agriculture with no trees, or wooded habitats with no open areas. In some extensively grazed regions, such as the Dehesas, agroforestry systems often form transitional zones between open grasslands and forests, thereby supporting communities characteristic of both ecosystems (Hartel and Plieninger 2014; Moreno and Pulido 2009).

This spatial heterogeneity of agroforests is driven by the interplay of woody and herbaceous habitats. The presence of trees in agroecosystems strongly influences temperature, shading, humidity and wind speed (Stamps and Linit 1997; Smith et al. 2013; Quinkenstein et al. 2009), thereby modifying the ground-level microclimate, which in turn shapes the activity-density and composition of ground-dwelling spider communities (Entling et al. 2007; Wise 1993). For instance, Martin-Chave et al. (2019b) observed altered circadian activity in *Pardosa* sp. within silvoarable systems compared to treeless croplands, and this was explained by the mitigation of daily temperature extremes, these areas remaining cooler during the day and warmer at night. In these systems, vegetation strips beneath tree rows, combined with minimal disturbance (primarily from reduced tillage), create buffered microclimates and provide high-value food resources for spiders and other arthropods (Stamps and Linit 1997; Boinot et al. 2019; Geiger et al. 2009; Mestre et al. 2018; D’Hervilly et al. 2022; Pardon et al. 2019; Bentrup et al. 2019).

The presence of livestock also enhances the heterogeneity of agroforestry systems. In silvopastoral plots, the structure of the herbaceous layer is largely shaped by grazing animals. By introducing localized disturbances and creating successional differences at a fine spatial scale, grazing significantly alters vegetation structure, thereby influencing spider assemblages (Horvath et al. 2009; Gibson et al. 1992). Previous studies have demonstrated shifts in spider community composition under grazing systems (Hemm and Höfer 2012; Oyarzabal and Guimaraes 2021; Dennis 2003; Gibson et al. 1992; Horvath et al. 2009; Birkhofer et al. 2015a, b, c), supporting our findings of differences in spider assemblages between silvopastoral systems and ungrazed orchards, forests and silvoarable systems. Surprisingly, silvopastures were the only habitat type for which we found no indicator species. Thus, we did not detect any edge specialists that would be absent from the treeless or completely wooded control habitats – at least no such species that were frequent enough across countries to stand out significantly in our analysis.

Our study reinforces the link between spider communities and habitat type, highlighting the influence of vegetation structure. The spatial heterogeneity of agroforestry systems provides a mosaic of habitats at small spatial scales that accommodate species with diverse environmental requirements, allowing openland specialists to coexist alongside forest dwellers.

In line with their more distinct position in the ordination (Fig. 1), more indicator species were found for orchards and croplands than for pastures and agroforestry. The indicator species identified for cropland are widely known agrobionts: *Oedothorax apicatus* for cool temperate, and *Pardosa proxima* and *Diplocephalus graecus* for Mediterranean climate (Samu and Szinetár 2002; Isaia et al. 2018; Bach et al. 2023). *Oedothorax apicatus* was the only species with higher densities in crop plots than in semi-natural habitats even during winter (Mestre et al. 2018), which explains the strong association also shown in our study. The four indicator species of orchards are not typical agrobionts (Samu and Szinetár 2002). Nevertheless, according to Entling et al. (2007), they prefer relatively open habitats, which indicates a high disturbance level of the studied orchards despite the presence of trees. The presence of only one indicator species for forests is surprising and may reflect the high beta diversity of forests that is also reflected in their wider dispersion in Fig. 3. Highly distinct spider assemblages across the studied forests could preclude the emergence of widespread indicator species, which underlines a high conservation value of this relatively near-natural habitat. *Trochosa ruricola* and *Diplostyla concolor*, the two indicator species of silvoarable systems, are common in farmland, but overwinter mostly in perennial herbaceous vegetation (Mestre et al. 2018), which was present under the tree rows of the studied plots. The absence of indicator species for silvopastures suggests that they support few if any ecotone specialists, but rather a mix of species of grasslands and forest.

Spider diversity

Contrary to our expectations and contrary to previous studies, we found no strong correlation between spider α- or β-diversity and structural heterogeneity or grazing. Increased detritus and vegetation complexity within plots —promoted by practices such as polycultures, weed strips, shrubs, mulching, leaf litter, intercropping, or reduced tillage and mowing— have been shown to enhance ground-dwelling spider abundance (Langellotto and Denno 2004; Sunderland and Samu 2000) and diversity (Hemm and Höfer 2012). For example, Matevski et al. (2024) reported higher ground-dwelling spider abundance in silvoarable systems compared to cropland, probably explained by their greater habitat heterogeneity. Grazing management also plays an important role, as it affects vegetation structure and thereby shapes spider communities. A decrease in grazing intensity, which promotes higher and more structured complex vegetation, has been shown to increase spider species richness in grasslands (Horvath et al. 2009).

However, in line with our findings, some studies have also reported no effect of increased structural heterogeneity on spider species richness and diversity at plot scale. Moreno et al. (2016) did not measure any effect of Spanish silvopastures on spider species richness at plot scale, but these Dehesas supported more spider species due to their higher β-diversity and heterogeneity at the landscape scale compared to adjacent open pastures. Imbert et al. (2020) found no difference in spider abundance between silvoarable and arable plots, while Matevski et al. (2024) observed higher spider abundance in silvoarable fields but no significant differences in species richness. In this last study, α- and β-diversity were significantly higher in silvoarable systems than in croplands only at specific distances from trees (1 m and 7 m, respectively), but no overall differences were detected at the field level. Although species richness and taxonomic diversity are commonly used to assess the effects of land-use on spider diversity, studies have shown that patterns in species richness may not always align with patterns in the functional diversity of spider communities, both across habitat types and spatial scales (e.g. Birkhofer et al. 2015a, b, c; Joseph et al. 2018; Mahon et al. 2023; Pinto et al. 2021). The differences in community composition we observed could therefore also reflect differences in trait composition or functional diversity. However, our analysis of functional diversity revealed no significant differences between land-use types (results not shown).

The study by Matevski et al. (2024) highlights considerable variability in the distribution of ground-dwelling spiders in agroforestry systems, which may explain why we did not detect differences in species richness and diversity between agroforestry and other habitat types. The greater structural heterogeneity of agroforestry plots compared to more homogeneous control plots may reduce spider mobility while providing a wider range of suitable habitats. As generalist predators, spiders primarily move to find refuge, prey, and mates. If these needs are met within a confined space, their mobility decreases, potentially enhancing survival rates (Sunderland and Samu 2000; Mensah 1999). The increased substrate diversity in structurally complex habitats, such as agroforestry systems, may offer more shelter opportunities and facilitate prey location and mating. Wandering spiders, for instance, rely on substrate-borne vibrations, stridulations, and percussions for communication and mate-finding (Uetz and Stratton 1982). Additionally, spider prey—particularly meso- and macrofauna—may benefit from the organic material accumulation in agroforestry systems, leading to increased prey density near trees and vegetation strips. This higher prey availability could also reduce spider movement, as they need to travel less to locate food (Imbert et al. 2020). While vegetation corridors can enhance spatial connectivity and facilitate spider movement between isolated habitats (Baker 2007), structurally complex vegetation matrices have been shown to lower arthropod mobility due to increased habitat permeability compared to open plots (Frampton et al. 1995). Consequently, reduced spider mobility and their tendency to aggregate in undisturbed vegetation (Thorbek and Bilde 2004) may have contributed to lower capture rates in agroforestry plots (Curtis 1980).

Reduced mobility on their complex ground surface may also explain the unexpectedly low spider diversity and species richness observed in forests, which typically support the highest spider abundance and diversity across ecosystems. Forest canopies and understory layers can host significant spider biomass, with at least 20% of total biomass occurring above ground level (Nyffeler and Birkhofer 2017). Thus, the relatively low spider species richness in forests should be interpreted with care, since it cannot be determined from our study whether it is due to truly reduced α-diversity or due to less complete sampling in forests compared to more open habitats. We suspect that a complete sampling of all layers would reveal stronger contrasts between the habitats involving trees (forests, orchards, silvoarable and silvopastoral agroforestry) and the open cropland and pasture habitats (Jeanneret et al. 2022), although generally less spider species in Central Europe appear to be adapted to forest compared to open land (Entling et al. 2007).

Our study revealed considerable variability in species richness and diversity among plots within each habitat type. Additionally, community composition and β-diversity varied substantially across countries. These variations may be attributed to the climatic differences between our study regions. Three sites each were in the Mediterranean and Continental biogeographic regions, and the two other sites in the Atlantic biogeographic region, reflecting a broad environmental gradient across Europe (Roekaerts 2002). This geographic distribution likely influenced local species pools, land-use history, and ecological processes, contributing to the observed heterogeneity in arthropod communities.

In addition, there were differences in tree and crop species, livestock types, and management practices across sampled sites. Various tree characteristics, including age, density, diversity, and species identity, influence microclimatic conditions and the quantity and quality of litter, thereby shaping arthropod and spider communities (Pardon et al. 2019; Sobek et al. 2009; D'Hervilly et al. 2022; Martin-Chave et al. 2019a, b; Ziesche and Roth 2008). Moreover, management practices such as mowing, grazing intensity, tree cutting, and pruning affect canopy openness and ground microclimate, exerting strong effects on ground-dwelling spider assemblages (Gardner et al. 1995; Martin-Chave et al. 2019b; Quinkenstein et al. 2009; Cattin et al. 2003; Hemm and Höfer 2012).

Interestingly and in line with our results, Lüscher et al. (2014) in a pan-European study found a high effect of geographic location and plot management on spider diversity and composition but they measured no effect of surrounding landscape. These findings highlight the importance of local management in shaping arthropod biodiversity, often outweighing broader landscape influences. Thus, the pronounced regional differences observed in spider communities are not unexpected, given the environmental and management heterogeneity across our study sites. More consistent patterns might emerge in studies restricted to a single biogeographic region with more uniform management regimes. However, by including country as a random effect in our analysis, we accounted for regional variability. Overall, our results indicate that agroforestry does not lead to consistent changes in species turnover of ground-dwelling spiders—either within or between plots—across Western and Southern Europe.

Finally, we found a marginally significant decrease in spider species richness with increasing field size, independently of habitat type. This aligns with previous studies demonstrating the positive effect of reducing crop field size on multitrophic diversity, including spiders (Batáry et al. 2017; Fahrig et al. 2015; Šálek et al. 2018; Sirami et al. 2019; Tscharntke et al. 2021). Small field size can facilitate spider immigration and spillover from field edges and neighboring habitats (Schmidt et al. 2008; Schmidt and Tscharntke 2005). In addition, the proximity of different habitat types can facilitate the use of multiple complementary resources by spiders, such as flying insect prey from different ecosystem types (Middendorf et al. 2025). Small field sizes increase the density of ecosystem boundaries in a landscape, which has been shown to enhance connectivity and overall diversity of spiders and other taxa at the landscape scale (Holland and Fahrig 2000; Gavish et al. 2012). Additionally, increased crop diversity and the presence of seminatural habitats at the landscape scale have been shown to positively influence biodiversity, although the relative strength of these effects compared to field size reduction varies across studies (Fahrig et al. 2015; Sirami et al. 2019; Šálek et al. 2018). Our findings confirm the complementary roles of field size and presence of trees in biodiversity conservation: while smaller fields promote higher species richness, the increased heterogeneity provided by agroforestry systems widens the range of habitat conditions to include forest-adapted species.

Conclusions and management implications

Agroforestry systems create an ecological setting where open and wooded habitats coexist in close proximity—an uncommon feature in many of today's European agricultural landscapes. Our study demonstrated that this structural heterogeneity facilitates the coexistence of spider species with different habitat preferences, providing essential resources for both open-land and forest-dwelling species. As such, agroforestry systems may function as ecological corridors or "extended ecotones" within agricultural landscapes, promoting species movement between habitat fragments and buffering protected areas from the impacts of intensive agriculture (Diaz et al. 2013).

While β-diversity was similar across habitats, our findings indicate that agroforestry systems enhance overall biodiversity at the landscape scale by hosting distinct spider communities. Thus, agroforestry seems an ideal component of agricultural diversification for biodiversity. Our study showed that the highest overall spider diversity at landscape scale would be supported by a mosaic of small habitats, each associated with distinct management practices and vegetation structures (e.g., wooded, open, grazed, and non-grazed areas).

However, the benefits of agroforestry for spiders appeared less pronounced than those observed for other taxa such as bats and birds (Edo et al. 2024, 2025). This underlines the high ecological amplitude and diversity of spiders, which occur in considerable species richness, even in intensive agricultural fields. These findings underscore the importance of considering multiple taxonomic groups when assessing the ecological value of land-use strategies. Different taxa may respond in contrasting ways to habitat features and management practices. Therefore, a multi-taxa approach is essential for identifying complementary conservation strategies that effectively promote biodiversity in agricultural landscapes.

Acknowledgements We would like to thank our colleagues from the AGROMIX project—Mickael Bernard, María Blanco Gutierrez, Samuele Ciacci, Lydie Dufour, Marco Gentili, Samuel Hepner, John Kearns, Rachael Ramsey, Robin Russias, and Sophie Tournier—for their collaboration and support. We are also grateful to the students Jonas Federkeil and Anja Weiler for their assistance with data collection. Special thanks go to the landowners who kindly allowed us to sample on their farms. We extend our sincere thanks to Sebastian Kolb for his invaluable assistance with spider identification, and to Johan Van Keer for his support in identifying the Scytodes species. We also thank Sylvain Déjean, Nicolas Hénon, Christophe Mazzia, and Etienne Lorio for kindly providing spider specimens and sharing their knowledge about specific spider species. We also thank the reviewers and the editor for their comments, which helped improving this manuscript.

Author contributions Manon Edo, Felix Herzog, Gerardo Moreno, Rodrigo Olave, Will Simonson and Martin H. Entling contributed to the study conception and design. Manon Edo, Rodrigo Olave, Alice Ripamonti, Will Simonson and Lorenzo Gabriele Tramacere collected the data. Manon Edo and Martin H. Entling analyzed the data. The first draft of the manuscript was written by Manon Edo and all authors commented on previous versions of the manuscript. All authors read and approved the final version of the manuscript.

Funding Open Access funding enabled and organized by Projekt DEAL. This research was part of the AGROMIX Project and received funding from the European Union's Horizon 2020 research and innovation program under grant agreement 862993.

Data availability The datasets as well as the codes generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors declare no competing interests.

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