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Mediterranean alley-cropping agroforestry modifies arthropod temporal dynamics with divergent effects on trophic groups

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ABSTRACT

Agroforestry is promoted as a sustainable agricultural practice that enhances biodiversity and ecosystem services, including natural pest control. However, its effects on arthropod communities, particularly across different trophic groups and seasonal dynamics, remain poorly understood. In this study, we assessed the impact of a Mediterranean alley-cropping agroforestry system on the abundance, diversity, and community composition of eight arthropod trophic groups, in Southern France. Using pan traps and pitfall traps, we sampled arthropods in agroforestry alleys and tree rows at three dates in spring 2023 (April, March and May), comparing them to monocultures and tree plantations. After identification, invertebrate taxa were classified into eight trophic groups based on current ecological knowledge. Agroforestry influenced arthropod abundance and diversity, though responses varied among trophic groups. Community composition, as reflected through a Principal Co-ordinates Analysis, was primarily structured by phenology rather than habitat type, with pronounced seasonal shifts across most trophic groups. Effect size analysis showed that tree rows supported a higher abundance of certain beneficial arthropods, emphasizing their role in agroforestry system function. Further research on multi-trophic interactions and long-term dynamics is needed to optimize agroforestry as a strategy for ecological intensification.

1. Introduction

In intensive agriculture, pesticides are widely used to control invertebrate herbivores, plant parasitoids (phytoparasitoids), and disease vectors (phytopathogens) (Dix et al., 1995). However, their extensive application raises significant concerns for both human health and the environment. Pesticide residues frequently contaminate soil and water, posing risks to human health by increasing the likelihood of various diseases (Bernardes et al., 2015; Nicolopoulou-Stamati et al., 2016). Furthermore, although pesticides are designed to target specific pests, they also impact non-target organisms, such as pollinators and other beneficial organisms (Landis et al., 2000; Bentrup et al., 2019; Bianchi, 2022). Over time, their effectiveness is reduced due to the development of pesticide resistance, further challenging sustainable pest management (Dix et al., 1995).

Beyond pesticide use, landscape simplification and intensive agricultural practices such as deep tillage and crop homogenization have led to a reduction in plant and habitat diversity, contributing to biodiversity decline in agroecosystems (Dudley and Alexander, 2017). These changes negatively affect arthropod populations, as well as birds and mammals, particularly those involved in key ecosystem services such as pollination, decomposition of organic matter, and biological pest control (Begg et al., 2017; Boinot et al., 2020; Landis et al., 2000). By altering ecosystems and disrupting natural interactions between plants and animals, intensive agriculture may weaken natural pest control mechanisms, reducing the efficiency of predator- and parasitoid-mediated regulation

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(Zhao et al., 2015). Approaches fostering reduced pesticide use and greater habitat/landscape heterogeneity are required to improve this situation.

Agroecological practices, which emphasize nature-based solutions, offer promising alternatives to mitigate the negative impacts of intensive agriculture while promoting biodiversity and ecosystem services (Staton et al., 2021). Among these practices, increasing plant diversity and preserving natural habitats within agricultural landscapes have been identified as key strategies to enhance ecological resilience (Begg et al., 2017). Agroforestry, which integrates trees into agricultural systems, emerges as a particularly promising approach to balance and sustain crop productivity while preserving ecosystem functioning. Successful in the tropics, this approach has proven effective in reconciling agricultural productivity with the preservation of biodiversity and key ecosystem functions. (Steffan-Dewenter et al., 2007; Clough et al., 2011; Marsden et al., 2020).

Agroforestry is characterized by three fundamental principles (Somarriba, 1992): (1) the coexistence of at least two interacting plant species, (2) the presence of at least one woody perennial species, and (3) the management of at least one species for fodder, annual, or perennial crop production. This practice offers numerous benefits, including improved soil fertility, reduced erosion, enhanced carbon sequestration, better water retention, microclimate regulation, soil suppressiveness to plant-parasitic nematodes and increased organic matter (Jose, 2009; Boinot et al., 2020; Jaworski et al., 2023; Masson et al., 2025). Within cultivated fields, trees create new habitats by increasing plant diversity, spatial heterogeneity, and resource availability, ultimately supporting a greater diversity of organisms (Martin-Chave et al., 2019; N'Woueni and Gaoue, 2022). By promoting animal diversity, agroforestry has the potential to encourage beneficial organisms such as pollinators, detritivores and granivores, thereby promoting pollination, decomposition of organic matter and weed seed regulation (Boinot et al., 2019). Changes in species abundance and diversity within agroforestry systems are driven by both bottom-up (resource availability) and top-down (predation pressure) mechanisms (Pumariño et al., 2015; Jaworski et al., 2023). Trees can enhance natural pest control by providing refuges and alternative food resources, fostering a greater diversity of predators and parasitoids (Letourneau et al., 2011; Staton et al., 2019; Boinot et al., 2020). However, they may also support generalist herbivores, which could feed on both trees and crops, potentially offsetting these benefits (Chaplin-Kramer et al., 2013; Silva et al., 2020).

Despite increasing evidence of agroforestry's positive effects on ecosystem functioning, research on trophic interactions and community dynamics in these systems remains limited (Pumariño et al., 2015; Isbell et al., 2017; Marsden et al., 2020). Most studies focus on a single group, such as soil fauna or pollinators, rather than considering the full spectrum of trophic interactions (Shameer and Hardy, 2024). While seasonality and phenology is an important element in arthropod population dynamics, few studies have evaluated the impact of agroforestry at various times during crop growth (Martin-Chave et al., 2019). Additionally, many agroforestry studies are conducted in tropical regions, particularly on perennial crops such as coffee or cocoa (Pumariño et al., 2015; Marsden et al., 2020). Given that agroforestry outcomes depend on factors such as crop type, tree species, and spatial arrangement, more research is needed to assess its impacts across diverse climatic and agricultural contexts. For instance, while agroforestry has been shown to significantly improve pest control in perennial crops, results remain inconclusive for annual crops (Pumariño et al., 2015). Trees and annual crops each have their set of pests and regulators, and in agroforestry systems their potential interactions throughout the cropping season deserve to be studied. Another important feature of agroforestry systems is that the absence of tillage beneath tree rows promotes the development of herbaceous strips that enhance biodiversity and offer refuges for beneficial organisms (Boinot et al., 2020; D'Hervilly et al., 2022).

Despite increasing evidence that agroforestry enhances biodiversity and ecosystem services, several knowledge gaps remain. Most studies are taxonomically limited, and the temporal dynamics of arthropod communities remain largely unexplored. Moreover, Mediterranean systems—subject to strong climatic constraints—are underrepresented in global syntheses. Addressing these gaps requires integrative approaches that jointly assess the spatial and temporal components of biodiversity across multiple trophic groups. In this study, we aimed to investigate how tree presence in Mediterranean agroforestry systems influences arthropod community composition (both taxonomic and trophic), and the related potential ecosystem functions. Our overarching hypothesis is that tree presence in alley-cropping agroforestry systems reshapes arthropod community composition and temporal dynamics by modifying habitat complexity, resource diversity, and microclimatic conditions. We formulated a set of precise hypotheses.

(i) By providing additional resources and microhabitats, trees and understory vegetation in agroforestry support higher arthropod abundance and diversity than adjacent monocultures.
(ii) The temporal composition of arthropod communities follows plant phenology, with peak abundances tracking crop and tree flowering and growth stages. Within this framework, herbivores are expected to show guild-specific temporal differentiation across habitats. Sap feeders may respond positively or remain stable depending on resource availability and microclimatic buffering. Leaf-chewing herbivores could decline under increased predation or reduced herbaceous resources, yet benefit from greater plant diversity. Ground-dwelling granivores (herein viewed as beneficial organisms) should peak in open crop monocultures dominated by seed-producing annuals.
(iii) By offering refuges and alternative prey or hosts, agroforestry is expected to stabilize or enhance populations of natural enemies (predators and parasitoids), thereby strengthening biological control of herbivores. We predict higher abundance and diversity of these groups in tree-structured habitats compared to open-habitat, with two different temporal dynamics, reflecting a more complex and resilient multi-trophic networks.
(iv) Beyond herbivory pressure and its trophic regulation, increases in structural and resource heterogeneity by tree presence and understory vegetation are expected to benefit detritivores and pollinators, which rely on litter resources and floral continuity.

2. Material and method

2.1. Design of the agroforestry trial

2.1.1. Study site

The study was conducted at the DIAMS experimental agroforestry site (*Dispositif Instrumenté en Agroforesterie Méditerranéenne sous contrainte hydrique*) in Mauguio (43.612°N; 3.976°E), Southern France. The climate is Mediterranean, with dry summers and an average annual precipitation of 526 mm (varying from 248 to 908 mm) between 2014 and 2023. The 12 months prior to the sampling sessions had normal precipitation, with 543 mm from March 2022 to February 2023. The soil is a skeletic rhodic Luvisol (IUSS Working group WRB 2014), with a high but variable stone content (up to 60 %) and a decarbonated surface layer (pH varying from 6.5 to 8). The site is organized into three blocks, each serving as a replica. Within each block, three plot types were established: a monoculture crop (MC), a tree plantation (TP), and an agroforestry plot (AF) (Fig. 1). The experimental area covers a total of 5 ha. Plot sizes vary slightly among blocks: Block 1 – TP = 0.12 ha, MC = 0.16 ha, AF = 0.31 ha; Block 2 – TP = 0.09 ha, MC = 0.16 ha, AF = 0.31 ha; Block 3 – TP = 0.09 ha, MC = 0.12 ha, AF = 0.31 ha.

2.1.2. Criteria for tree selection and experimental layout

Robinia pseudoacacia L., 1753 was chosen as the tree species based on a combination of ecological and practical criteria (Mantovani et al., 2014). Priority was given to rapid-growth, nitrogen-fixing species

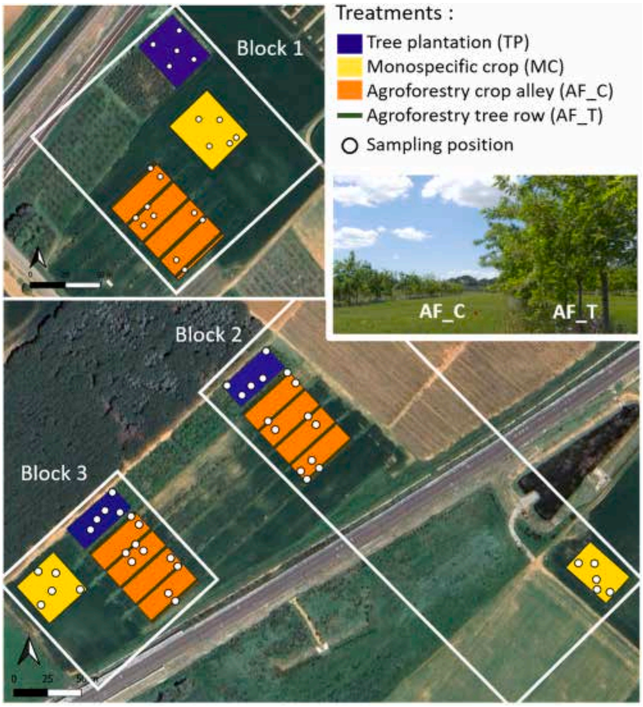

Fig. 1. Map of the DIAMS experimental site (*Dispositif Instrumenté en Agroforesterie Méditerranéenne sous contrainte hydrique*) in Mauguio, Hérault, France. Pitfall and pan traps were set in March, April and May at the 60 sampling positions, distributed equally between the three blocks and the four different treatments. The photograph of an agroforestry plot, taken in 2023, illustrates the difference between the cultivated alley (AF_C) and the row of trees (AF_T).

capable of thriving under Mediterranean climatic conditions. Additional selection criteria included compatibility with surrounding agricultural practices, the ability to provide structural heterogeneity and refuge habitats, and the production of durable, high-value wood to ensure long-term economic viability. In Mediterranean agroforestry systems, the range of suitable nitrogen-fixing trees is extremely limited: *Acacia* species are invasive and not naturalized in France, while *Alnus* species are poorly adapted to dry climates. *R. pseudoacacia*, naturalized in Europe for over three centuries, offers a pragmatic compromise. Its open canopy structure provides refuge habitats for open-habitat arthropods, (including some endangered species in Czech Republic; Štrobl et al., 2019), a property desirable in our intensively managed agricultural landscape. In addition, its low germination rate, limited vegetative spread (controlled by tillage), and high-value, durable wood make it a “win–win” species for both production and biodiversity goals.

In both AF and TP plots, *R. pseudoacacia* trees were planted between 2017 and 2018. The agroforestry plots consist of monoculture crops interspersed with tree rows spaced 17 m apart. In the TP plots, tree rows are spaced 3 m apart, and on each row in both AF and TP plots, trees are spaced every 2 m. During the study period, spring barley (*Hordeum vulgare* L., 1753) was grown in both the MC and AF plots. The previous crops were pea and durum wheat, harvested in 2022 and 2021 respectively. While no insecticides were applied, a herbicide treatment was carried out in March, and nitrogen mineral fertilizer was applied twice: 50 kg.ha^{-1} in March and 40 kg.ha^{-1} in April 2023, in both MC and AF plots. The barley crop was harvested in July 2023, with an average yield of 1.8 t.ha^{-1} .

In the agroforestry system, a distinction was made between the centre of the cultivated alleys (AF_C) and the tree rows (AF_T). In both TP and AF_T, the absence of tillage and herbicide application allow spontaneous grass to develop beneath the trees. This understory vegetation plays a significant role in the system, and its effects cannot be entirely separated from those of the trees. Consequently, the study assessed (i) the combined impact of tree rows and understory vegetation on the cultivated portion of the AF system by comparing arthropod communities in AF_C and MC treatments and (ii) the influence of the surrounding crop on the tree rows by comparing arthropod communities beneath the trees in TP and AF_T.

2.2. *Arthropod sampling*

Sampling was conducted three times throughout the season, on March 14, April 17, and May 24, 2023, corresponding to three phenological stadia of the crop (tillering, stem elongation and heading). Five micro-plots (4 m2) were placed in each experimental plot in the forest (F) and monoculture (MC) treatments. In the agroforestry (AF) treatment, five semi-permanent micro-plots were established beneath the tree rows and five within the cropped inter-row. Arthropod communities were sampled using two types of traps, pan traps for flying insects (e.g. pollinators, flying herbivores, parasitoids) and pitfall traps for ground-dwelling arthropods (e.g. detritivores, ground-dwelling predators). In each of the four treatments (MC, AF_C, AF_T, and TP) within the three blocks, one trap of each type was installed in every micro-plot, resulting in a total of 60 traps per method. Pan traps consisted of 30 cm diameter yellow containers (Jalonnet, ref: JALO 58629) filled with 1 litre of water and a few drops of dishwashing liquid to break surface tension (Vrdoljak and Samways, 2012). Each pan trap was positioned at the height of the surrounding vegetation—either within the herbaceous layer under the trees or at the barley canopy level in cultivated plots—to optimize insect capture (Tuell and Isaacs, 2009). Pitfall traps were 5 cm diameter plastic pots, buried flush with the soil surface and filled to two-thirds with vinegar (Hedde et al., 2013). To protect against weather conditions and evaporation, each pitfall trap was covered with a Plexiglas roof. Pan traps were deployed for 48 h, and pitfall traps remained in place for 7 days (Staton et al., 2021; Trisnawati et al., 2022).

2.3. *Identification and classification*

The identification and classification of arthropods followed a multi-step approach, including specimen preservation and sorting, taxonomic identification at the finest feasible level, expert validation through iNaturalist, and subsequent assignment of each taxon to a trophic group. Invertebrates were classified into eight trophic groups to encompass the diversity of organisms contributing directly or indirectly to ecosystem regulation: sap feeders, leaf feeders, parasitoids, flying predators, ground-dwelling predators, pollinators, detritivores, and granivores. In the present paper, for the sake of clarity, we named ‘leaf feeders’ a group of herbivores that primarily consume leaves but can also feed on lichen or stems for example. While the study primarily focused on natural enemies and herbivores, the inclusion of additional groups was necessary to account for alternative prey-supporting predator populations, taxa involved in resource regulation such as post-dispersal granivores, and those contributing to organic matter recycling (detritivores) or to pollination (pollinators). These steps are detailed hereafter.

2.3.1. *Specimen sorting*

After collection, all arthropods were preserved in ethanol and subsequently sorted in the laboratory. Some specimens were removed from the dataset because they did not fit the study’s objectives or were poorly represented by the sampling method (for example, Araneae and larval stages occasionally caught in pan traps). Two large and taxonomically complex groups, Diptera (except Syrphidae) and Staphylinidae, were also excluded due to their very high diversity and the absence of sufficient identification expertise. In total, the analyses were based on roughly 30,000 individuals, representing 61.3 % of all specimens collected.

2.3.2. *Specimen identification*

Invertebrates were identified using a Wild Makroskop 420

1.25 × binocular magnifier. Due to the wide taxonomic diversity of collected specimens, not all individuals could be identified to the same taxonomic level. Therefore, the level of identification of each specimen depended on both the identification capacity and the level required for trophic assignment. For instance, within the Hemiptera, aphids (Aphididae) and leafhoppers (Cicadellidae) —predominantly herbivorous— were identified at the family level, whereas true bugs (Heteroptera), which display a broad range of diets, were mostly identified at the genus or species level to better capture functional heterogeneity.

Three taxa comprising numerous individuals but difficult to identify beyond order level— Psocodea, Thysanoptera —, or super-family level —Psylloidea—were treated as a single operational taxon, and included in analyses at family level. Because they are largely or entirely represented by species sharing similar trophic habits, their inclusion at this level is expected to induce low bias in the conclusions.

Concerning some of the most diverse/abundant groups, we used Vandel (1962) and Noël et al. (2022) for Isopoda, Korsós and Lazányi (2020) for Diplopoda, Gloor et al. (2010) for Araneae, Blatrix et al. (2013) for Formicidae, Coulon et al. (2011) for Carabidae, Chemyreva and Kolyada (2021), Hübner et al. (2023), Hübner and Chemyreva (2024), Macek (1995, 1996, 2000) and Nixon (1980) for Diapriidae, Broad et al. (2018) and specific keys for ichneumonid wasps. These identification keys, some of which are partially outdated, were used as foundational references and supplemented with more recent sources.

2.3.3. *Expert validation*

To improve our lab identification accuracy, selected specimens were photographed using a binocular microscope equipped with a 20MP USB3.0 CMOS camera. These images were uploaded to iNaturalist, allowing both amateur and professional naturalists to contribute expertise and to refine taxonomic identifications. The verified identifications from iNaturalist were checked to ensure that the verifications were correct and were incorporated into the dataset in May 2025. The related iNaturalist project is available at this link: https://www.inaturalist.org/projects/diams_global. The current French taxonomic referential, TaxRef v18, was mostly used as a standard for taxonomy (Gargominy, 2025). In total, about 10 % of individuals were identified to class level (mostly larvae), 31 % to order, 34 % to family, 7 % to genus, and 18 % to species level.

2.3.4. *Classification*

Arthropods were assigned to trophic groups using a combination of expert-based and interaction-based inference. Flying taxa from pan traps were queried through the GloBI API to extract recorded interactions (e.g. eats, pollinates, parasitoidOf) while ground-dwelling taxa from pitfall traps were classified using both GLoBI and the SLIME knowledge graph (https://github.com/nleguillarme/SLIME). When missing, information was seek in the literature. Interaction types were then collapsed into major trophic roles (animal feeder, plant feeder, detritivore, pollinator, parasitoid), complemented by taxonomic information at family and genus levels. The flying arthropods collected with pan traps encompassed predators, parasitoids, pollinators, sap feeders and leaf feeders (i.e. flying chewers that consume leaves or other plant organs, lichen, or fungi). For ground-dwelling arthropods captured using pitfall traps, we distinguished soil-dwelling predators, detritivores, and granivores (i.e., post-dispersal granivores). The final classification included eight trophic groups, obtained by separating flying and ground-dwelling insects, and distinguishing between three groups of herbivores —sap feeders, granivores and leaf feeders— that have different feeding habits, and therefore different impacts on crops (Table 1).

2.4. *Statistical analyses on community metrics*

Out of 360 samples, three pan traps were excluded from the analyses: one identified as an outlier based on a z-score test, and two others lost due to a storm. Additionally, one pitfall trap was lost in the field.

Table 1

Families and orders of our dataset included in each trophic group. Taxonomic orders are highlighted in **bold**, while their respective families are listed in parentheses.

Trophic group	**Orders** (families)
Pollinators	**Coleoptera** (Buprestidae, Cantharidae, Cerambycidae, Chrysomelidae, Cleridae, Dermestidae, Melyridae, Mordellidae, Nitidulidae, Oedemeridae, Phalacridae, Scarabaeidae, Scraptiidae); **Diptera** (Syrphidae); **Hymenoptera** (Andrenidae, Apidae, Colletidae, Halictidae, Megachilidae, Pompilidae, Sphecidae, Tenthredinidae, Vespidae); **Orthoptera** (Tettigoniidae)
Detritivores	**Coleoptera** (Anthicidae, Cryptophagidae, Dermestidae, Elateridae, Eucinetidae, Nitidulidae, Scarabaeidae); **Hemiptera** (Pyrrhocoridae); **Isopoda** (Armadillidiidae, Porcellionidae); **Julida** (Julidae)
Granivores	**Coleoptera** (Carabidae); **Hemiptera** (Pyrrhocoridae, Rhyparochromidae); **Hymenoptera** (Formicidae)
Sap feeders	**Hemiptera** (Aphididae, Aphrophoridae, Cicadellidae, Coreidae, Delphacidae, Lygaeidae, Miridae, Pentatomidae, Psylloidea, Tingidae); **Thysanoptera**
Leaf feeders	**Coleoptera** (Brentidae, Buprestidae, Chrysomelidae, Curculionidae, Elateridae); **Hymenoptera** (Argidae, Tenthredinidae); **Orthoptera** (Acrididae); **Psocodea**
Flying predators	**Coleoptera** (Anthicidae, Cantharidae, Carabidae, Cleridae, Coccinellidae, Histeridae, Melyridae); **Diptera** (Syrphidae); **Hemiptera** (Anthocoridae, Miridae, Reduviidae); **Hymenoptera** (Ampulicidae, Crabronidae, Pemphredonidae, Pompilidae, Sphecidae, Vespidae); **Orthoptera** (Tettigoniidae)
Soil-dwelling predators	**Araneae** (Agelenidae, Amaurobiidae, Araneidae, Dysderidae, Gnaphosidae, Hahniidae, Linyphiidae, Liocranidae, Lycosidae, Philodromidae, Salticidae, Synaphridae, Theridiidae, Thomisidae, Titanoecidae, Zodariidae); **Coleoptera** (Anthicidae, Carabidae, Coccinellidae, Histeridae, Melyridae); **Hemiptera** (Nabidae, Pyrrhocoridae); **Hymenoptera** (Formicidae); **Opiliones** (Phalangiidae)
Parasitoids	**Hymenoptera** (Aphelinidae, Bethylidae, Braconidae, Ceidae, Ceraphronidae, Chalcididae, Chrysididae, Diapriidae, Dryinidae, Encyrtidae, Eulophidae, Eupelmidae, Eurytomidae, Figitidae, Ichneumonidae, Megaspilidae, Mymaridae, Pirenidae, Platygastridae, Proctotrupidae, Pteromalidae, Scelionidae, Spalangiidae, Tetracampidae, Tiphiidae, Torymidae, Trichogrammatidae)

For each trophic group, we analysed the total arthropod activity-density, as a proxy for abundance, according to treatments (MC, AF_C, AF_T, and TP) and sampling month, using Generalized Linear Mixed Models (GLMMs) fitted with the negative binomial distribution in the *glmmTMB* package to account for overdispersion (Brooks et al., 2017). Abundances were pooled across traps within each treatment and month. We included the block as a random effect and tested more complex random structures (block/treatment), but they did not improve model fit according to AIC. We therefore assessed the effects of treatment, month, and their interaction which were included as fixed effects, while block was included as a random effect. This was the most parsimonious model structure. Model fit was assessed using DHARMa residual diagnostics (Hartig, 2024). Then, Analysis of Deviance using Type II Wald chi-square tests was performed to assess the significance of fixed effects in the models (*car* package; Fox and Weisberg, 2019), followed by Tukey HSD pairwise comparisons using estimated marginal means (*emmeans* package; Lenth et al., 2025) to examine both between-treatment and between-month differences. For the three main sap-feeding taxa (Aphididae, Thysanoptera, and Psylloidea), differences in abundance across treatments were tested using GLMMs for each month, since the complete model did not adjust due to very high differences between months. An analysis of deviance was then performed on these models.

Taxonomic diversity within trophic groups was assessed at the family level to maximize taxonomic precision while minimizing data loss from unidentified specimens. We used the Hill numbers framework, which provides an asymptotic modeling approach to quantify diversity (Chao et al., 2014). Hill numbers offer a unified framework for measuring diversity by incorporating different sensitivity levels to taxa abundance. This approach models diversity as a function of the parameter q, which determines the weighting of species based on their relative abundance. In our study, we focused on Hill diversity with $q = 1$, which corresponds to the exponential of Shannon entropy. We used the *divent* package (Marcon, 2023). This metric considers the number of families, while weighting each family by its abundance. The choice of an asymptotic framework ensures that diversity estimations remain robust and comparable across samples, even when family detection probabilities vary (Coudrain et al., 2016; Hedde et al., 2024). Diversity values were then analyzed using generalized linear mixed models (GLMMs) implemented in the *glmmTMB* package, with a Gaussian error distribution. Model assumptions were assessed by testing for normality (Shapiro-Wilk test) and homogeneity of variance (Levene's test) and Analysis of Deviance using Type II Wald chi-square tests were performed to assess the significance of fixed effects in the models. A square root transformation was applied to all the trophic groups, except granivores, to normalize the data and improve model fitting.

To visualize the relative magnitude of treatment effects —on both activity-density and taxonomic diversity—, we calculated effect sizes as the log ratio of mean values in agroforestry habitats (AF_C and AF_T) and control habitats (MC and TP) for each trophic group and month. Specifically, comparisons were made between AF_C and MC to evaluate the impact of tree rows and understory vegetation on cultivated plots, and between AF_T and TP to assess how the surrounding crop influenced tree-line communities. This approach provides a standardized measure of the magnitude and direction of the effects, facilitating comparisons across different trophic groups and treatments.

To analyse and visualize temporal changes in community composition across trophic groups and treatments, trajectories were constructed by computing the Principal Coordinates Analysis (PCoA) positions of communities. These positions were based on the mean activity-density of each family per trophic group, month, and treatment, allowing for a dynamic representation of shifts in community structure over time. The distance matrix was calculated using the Bray-Curtis index with the vegdist function (*vegan* package; Oksanen et al., 2001). This approach highlights patterns of similarity or divergence among the four treatments, providing insights into how community composition evolves throughout the season.

All statistical analyses were performed using R (version 4.4.2) software (R Core Team, 2023). The *tidyverse* package (Wickham et al., 2019) was used to handle the data, which were visualized and represented using the *ggplot2* package (Wickham, 2016).

3. Results

3.1. Activity-density dynamics across trophic groups

The effects of treatment (MC, AF_C, AF_T, TP), sampling month (March, April, May), and their interaction on arthropod activity-density were analyzed across eight trophic groups (Table 2). The interaction between treatment and month was significant for sap feeders, leaf feeders, granivores, flying predators and pollinators ($p < 0.05$), indicating that the effects of agroforestry varied significantly over time for these groups. Thus, sap feeders and pollinators were significantly more abundant overall in cropped habitats (MC and AF_C) than in tree structured ones (AF_T and TP) ($p < 0.001$). Taking the three sampling dates into account, the abundance of granivores was significantly higher in monocultures (MC) on average ($p < 0.001$), while the abundance of leaf feeders was higher in the tree alleys of agroforestry plots (AF_T) ($p = 0.008$). In contrast, for other groups such as soil-dwelling predators, parasitoids, and detritivores, the interaction was not significant, so the effect of treatment remained consistent across months. Parasitoids were significantly more abundant in tree structured habitats (AF_T and TP) than in cropped ones (MC and AF_C) ($p < 0.001$). Detritivores were more abundant in the cultivated agroforestry alleys (AF_C) and tree plantations (TP) than in monocultures (MC) ($p = 0.001$). Soil-dwelling predators were significantly more abundant in monoculture (MC) ($p = 0.002$).

Table 2

Results of generalized linear mixed models (GLMMs) testing the effects of modality (MC, AF_C, AF_T, TP), sampling month (March, April, May), and their interaction (modality × month) on the activity-density of eight arthropod trophic groups. Chi-square (Chisq) values and significance levels (ns: not-significant; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$) are reported. Significant pairwise differences between modalities and months are indicated.

Trophic group	Term	Chisq	Significance	Differences
Sap feeders	treatment	137	***	MC, AF_C > AF_T, TP
	month	590	***	03 < 04 < 05
	treatment: month	36.1	***	
Leaf feeders	treatment	11.9	**	MC<AF_T
	month	2.32	ns	ns
	treatment: month	14.9	*	
Flying predators	treatment	1.82	ns	ns
	month	163	***	03 < 04 < 05
	treatment: month	13.5	*	
Soil-dwelling predators	treatment	15.3	**	MC>AF_C, AF_T, TP
	month	120	***	03 < 04 < 05
	treatment: month	12.2	ns	
Parasitoids	treatment	44	***	MC, AF_C < AF_T, TP
	month	461	***	03 < 04 < 05
	treatment: month	10.4	ns	
Granivores	treatment	20.3	***	MC >AF_C, AF_T, TP
	month	18.6	***	03, 04 < 05
	treatment: month	13.7	*	
Pollinators	treatment	23	***	MC, AF_C>AF_T, TP
	month	118	***	03 < 05 < 04
	treatment: month	12.9	*	
Detritivores	treatment	15.9	**	MC < AF_C, TP
	month	15	***	03 < 04,05
	treatment: month	5.31	ns	

A significant effect of the sampling month was detected for most groups, with a general increase in abundance from March to May ($p < 0.001$ for most groups). This trend was particularly pronounced for sap feeders, parasitoids, and predators, which showed a progressive increase over time (March < April < May). Granivores exhibited a delayed increase, with significantly higher abundance in May compared to March and April. Pollinators followed a different time pattern, with a peak in April followed by a decrease in May ($p < 0.001$). However, for sap feeders, leaf feeders, granivores, flying predators and pollinators, the temporal dynamics may differ depending on the treatment. The temporal variations in the mean activity-density of the three main herbivorous arthropod groups -Aphididae (aphids), Psylloidea (psylloids), and Thysanoptera (thrips)- is given on Fig. 2. The abundance of aphids remained low and statistically similar across all treatments in March and April (Fig. 2A). However, by May, there was a sharp increase, with tree plantations (TP) exhibiting the significantly highest aphid abundance, followed by tree alleys in agroforestry (AF_T) and cultivated agroforestry alleys (AF_C), which did not significantly differ from one another and finally monocultures (MC) exhibiting the lowest abundance (with mean abundance-activities of respectively 125.0 ± 37.0; 50.3 ± 13.0;

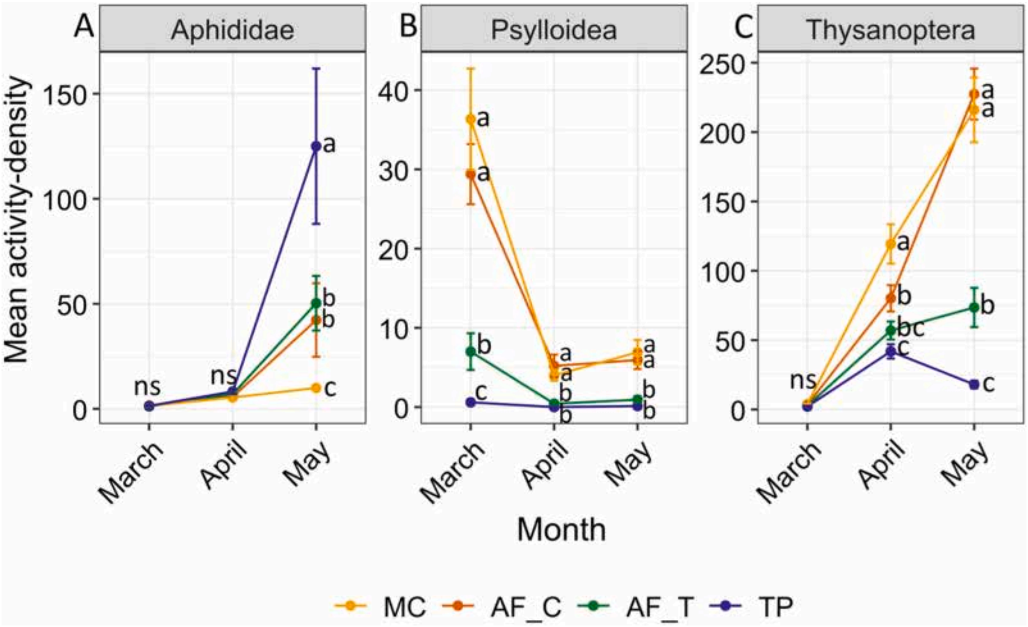

Fig. 2. Temporal dynamics of mean activity-density for three herbivorous arthropod groups (Aphididae, Psylloidea, Thysanoptera) sampled by pan trap across four agricultural treatments: AF_C (cultivated alley in agroforestry), AF_T (tree row in agroforestry), MC (monoculture), and TP (tree plantation). The x-axis represents the sampling months (March, April, May 2023), and the y-axis indicates the mean abundance per treatment. Different letters above data points indicate statistically significant differences among treatments within each month ($p < 0.05$), while "ns" denotes not-significant differences. Error bars represent standard errors.

42.3 ± 17.5 and 9.9 ± 1.1; $p < 0.001$). For psyllids, a distinct pattern was observed (Fig. 2B). In March, their abundance was significantly highest in cultivated plots (AF_C: 29.4 ± 3.8 and MC: 36.3 ± 6.4), intermediate in tree rows (AF_T: 7.0 ± 2.3), and significantly lower in tree plantations (TP: 0.6 ± 0.2) ($p < 0.001$). By April, psyllid abundance declined sharply across all treatments, and significant differences were observed between crops (MC and AF-C) and trees (TP and AF-T) ($p < 0.001$). This trend continued in May, when psyllid populations remained low across all treatments. Thrips populations exhibited a progressive increase over time (Fig. 2C). In March, their abundance was low across all treatments, with no significant differences detected. By April, thrips abundance increased significantly, with the highest values recorded in cultivated plots (AF_C and MC), intermediate values in tree rows (AF_T), and the lowest abundance values in tree plantations (TP) ($p < 0.001$). This pattern became even more pronounced in May, as thrips populations continued to rise, maintaining the highest levels in cultivated plots (AF_C and MC), followed by tree rows (AF_T), and remaining lowest in tree plantations, with mean abundance-activities of 227.4 ± 18.4 in AF_C; 216.0 ± 23.3 in MC; 73.5 ± 14.1 in AF_T and 18.0 ± 2.8 in TP ($p < 0.001$).

3.2. *Taxonomic diversity dynamics across trophic groups*

Sampled and analyzed individuals belonged to 4 classes and 11 orders. A total of 102 families, 333 genera, and 256 species were identified. The effects of treatment (MC, AF_C, AF_T, TP), sampling month (March, April, May), and their interaction on taxonomic diversity were analyzed for each trophic group (Table 3). The interaction between treatment and sampling month was significant for sap feeders, leaf feeders and pollinators ($p \leq 0.007$), indicating that treatment effects varied across months. No significant interaction was detected for the other trophic groups ($p > 0.05$), indicating relatively stable treatment effects over time.

A significant effect of treatment was detected for sap feeders, leaf feeders, and flying parasitoids ($p \leq 0.006$). Sap feeder diversity was significantly lower in MC compared to AF_T ($p = 0.001$), while leaf feeder diversity was higher in MC compared to TP ($p = 0.006$).

Table 3
Results of generalized linear mixed models (GLMMs) testing the effects of modality (MC, AF_C, AF_T, TP), sampling month (March, April, May), and their interaction (modality × month) on the taxonomic (family) diversity of eight arthropod trophic groups. Chi-square (Chisq) values and significance levels (ns: not-significant; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$) are reported. Significant pairwise differences between modalities and months are indicated. A square-root transformation was applied to all trophic groups except granivore.

Trophic group	Term	Chisq	Significance	Differences
Sap feeders	treatment	15.8	**	MC <AF_T
	month	25.3	***	04 < 03, 05
	treatment: month	40.4	***	
Leaf feeders	treatment	12.3	**	MC>TP
	month	79	***	03 < 04, 05
	treatment: month	17.7	*	
Flying predators	treatment	4.41	ns	ns
	month	175	***	03 < 04 < 05
	treatment: month	5.81	ns	
Ground-dwelling predators	treatment	1.17	ns	ns
	month	3.82	ns	ns
	treatment: month	11	ns	
Parasitoids	treatment	12.7	***	AF_C < TP
	month	232	***	03 < 04 < 05
	treatment: month	8.6	ns	
Granivores	treatment	5.85	ns	ns
	month	6.88	*	04 < 05
	treatment: month	10.8	ns	
Pollinators	treatment	6.33	ns	ns
	month	91.5	***	03 < 04 < 05
	treatment: month	53	***	
Detritivores	treatment	8.9	*	MC < TP
	month	3.81	ns	ns
	treatment: month	3.82	ns	

However, these differences in terms of diversity may differ depending on the month. Flying parasitoid diversity was significantly lower in AF_C compared to TP ($p < 0.001$). No significant effect of treatment was found for granivores, flying predators, soil-dwelling predators, or pollinators ($p > 0.05$). Finally, detritivores showed a higher diversity in TP compared to MC ($p = 0.031$).

A significant effect of the sampling month was observed for pollinators, leaf feeders, flying predators and flying parasitoids, with a progressive increase in diversity from March to May ($p < 0.001$ for most groups). Sap feeders showed a different pattern, with lower diversity in April compared to March and May ($p < 0.001$), while granivore diversity only increased between April and May ($p = 0.032$). However, for sap feeders, leaf feeders and pollinators, the temporal dynamics may have differed between the treatments. No significant temporal variation was observed for detritivores or soil-dwelling predators ($p > 0.05$).

3.3. *Log-ratio analyses*

The Log Response Ratios (LRR) of arthropod activity-density across trophic groups, comparing agroforestry to monoculture treatments are presented in Fig. 3. Two comparisons are shown: AF_C vs. MC, evaluating the effect of tree rows and understory vegetation on cultivated plots, and AF_T vs. TP, assessing how the presence of surrounding crops influences tree-line communities. For most trophic groups at a given period, confidence intervals overlap with zero, suggesting that the effects of agroforestry on activity-density are not consistently significant

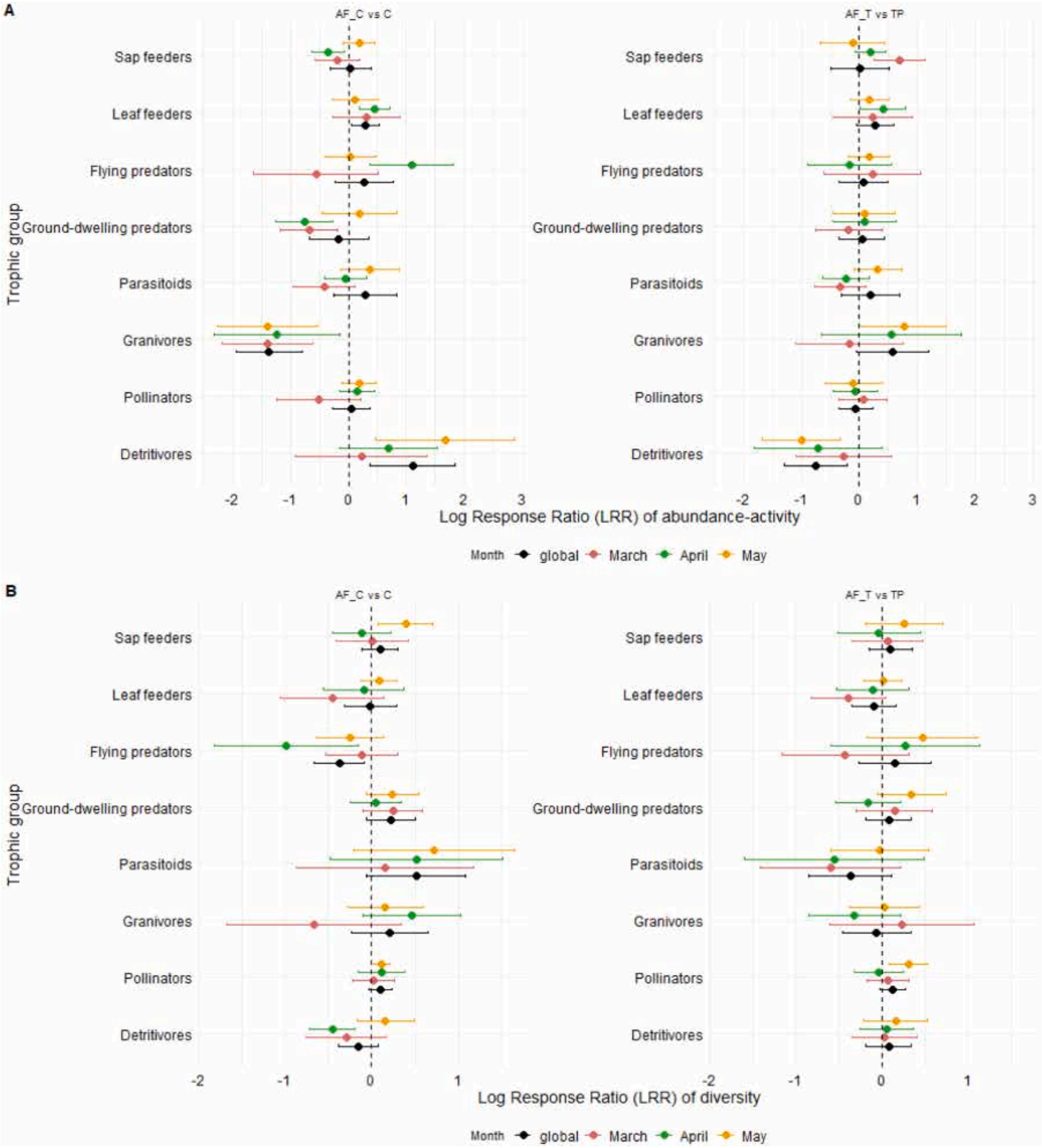

Fig. 3. Log Response Ratios (LRR) of arthropod activity-density (a) and diversity (b) across trophic groups in agroforestry and monoculture systems. The left panels (AF_C vs. C) compare the effects of tree rows and understory vegetation on cultivated plots, while the right panels (AF_T vs. TP) assess the influence of surrounding crops on tree-line communities. Points represent mean LRR values, with error bars indicating confidence intervals. Colors differentiate between overall effects (global) and monthly values (March, April, May). Positive values indicate higher activity-density (a) or diversity (b) in agroforestry treatments, while negative values indicate lower values relative to the corresponding control.

across treatments. However, some trophic groups exhibit clear trends, with variations across months indicating temporal fluctuations in the strength and direction of agroforestry effects. In the comparison between AF_C and MC, granivores and sap feeders tend to show negative LRR values, suggesting lower activity-density in agroforestry cultivated plots compared to monocultures. In contrast, detritivores and parasitoids exhibit a trend toward increased abundance in AF_C, though variation across months suggests that these effects are month-dependent. Other trophic groups, including pollinators, aerial and soil-dwelling predators, and leaf feeders, show variable or near-zero effects, indicating that tree rows and understory vegetation do not systematically influence their activity-density. In the AF_T vs. TP comparison, LRR values for most groups remain close to zero, indicating weak or inconsistent effects of surrounding crops on tree-row communities. Some positive trends are observed for flying predators and parasitoids, suggesting that agroforestry may favor certain predatory groups within tree rows. In contrast, granivores and sap feeders tend to show negative values, similar to the AF_C vs. MC comparison, suggesting lower activity-density in tree rows compared to tree plantations without adjacent crops. The monthly trends reveal fluctuations in LRR values, suggesting temporal effects on activity-density responses to agroforestry. Some groups, such as parasitoids and detritivores, exhibit stronger effects in April and May, whereas for others, such as granivores and sap feeders, negative responses appear more stable across months.

Fig. 3b presents the Log Response Ratios (LRR) for taxonomic diversity (family-level). For most trophic groups, confidence intervals overlap with zero, suggesting that the effects of agroforestry on taxonomic diversity are not consistently significant across treatments. However, some groups show distinct patterns, with temporal fluctuations affecting the strength and direction of agroforestry's impact. In the AF_C vs. MC comparison, the diversity of leaf feeders and sap feeders tends to be lower in agroforestry cultivated plots compared to monocultures, as indicated by negative LRR values. In contrast, detritivores and parasitoids exhibit positive LRR values, suggesting that their diversity may be enhanced by tree rows and understory vegetation. Other groups, including pollinators, aerial and soil-dwelling predators, and granivores, show variable or near-zero effects, indicating no clear impact of agroforestry on their diversity. In the AF_T vs. TP comparison, LRR values remain close to zero for most trophic groups, indicating weak or inconsistent effects of surrounding crops on tree-row communities. Some positive trends are observed for flying predators and parasitoids, suggesting that agroforestry may enhance diversity in these predatory groups. Conversely, sap feeders and granivores tend to show negative LRR values, mirroring the patterns observed in the AF_C vs. MC comparison. Monthly trends reveal fluctuations in LRR values, suggesting monthly variation in agroforestry's effects on taxonomic diversity. While parasitoids and detritivores show stronger positive responses in April and May, leaf feeders and sap feeders exhibit more consistent negative effects across months.

3.4. *Temporal dynamics of community composition*

The temporal trajectories of community composition for the eight arthropod trophic groups across the different treatments are displayed in Fig. 4. The ordination, based on Principal Coordinates Analysis (PCoA), represents variation in community structure using the two main axes of differentiation, with changes tracked over three sampling months (March, April, and May). The results reveal distinct temporal dynamics in community composition, with varying degrees of temporal change depending on the trophic group and agricultural treatment. For most groups, clear dynamics in community composition are observed over time, suggesting a response to temporal changes in the environment. However, the extent and direction of these shifts differ across trophic groups.

Among sap feeders, parasitoids and pollinators, progressive and structured shifts in community composition can be noticed over time,

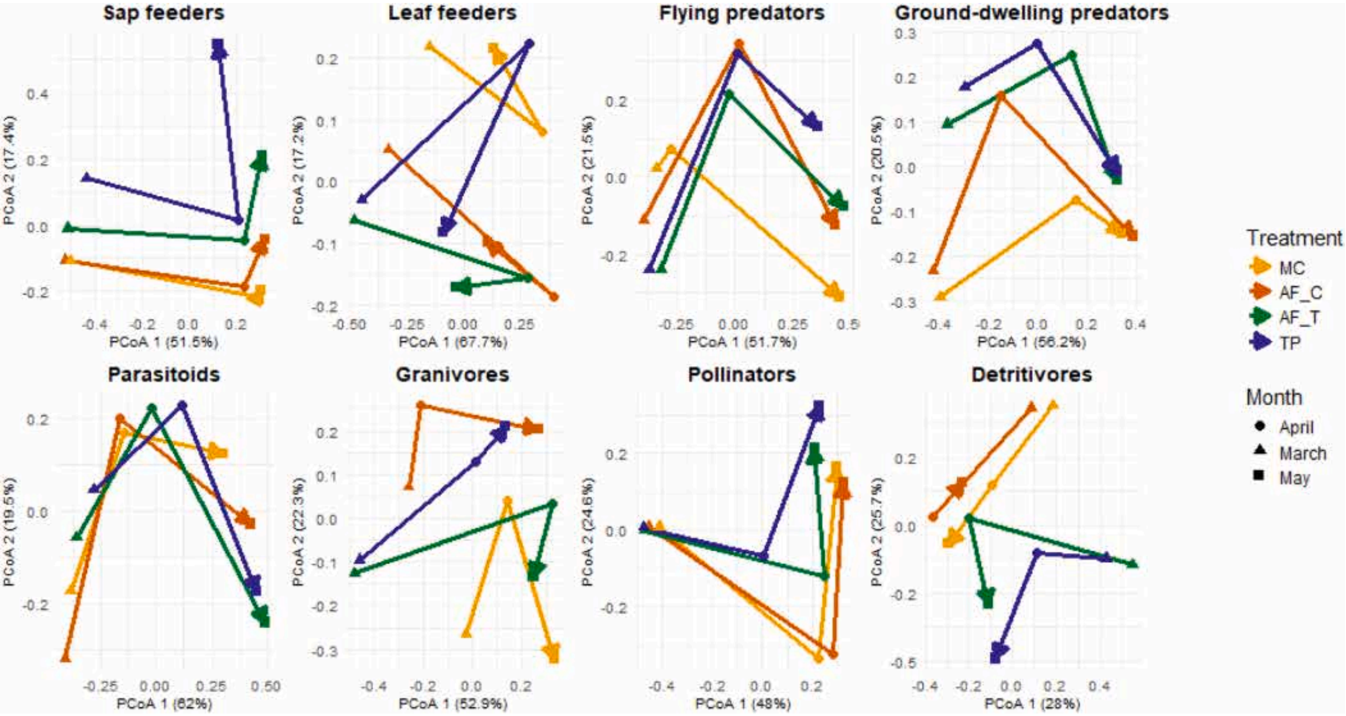

Fig. 4. Temporal trajectories of arthropod community composition across trophic groups and agricultural treatments. Principal Coordinates Analysis (PCoA) plots illustrate changes in community structure over three sampling months (March, April, and May) for eight trophic groups (sap feeders, leaf feeders, granivores, parasitoids, detritivores, flying predators, ground-dwelling predators, and pollinators). Each point represents the centroid of community composition for a given treatment and month, with lines connecting months sequentially to show temporal shifts. The two PCoA axes represent the main gradients of variation in community structure.

without deep differences between treatments, although MC and AF_C remain closer overall, as do AF_T and TP. Detritivores exhibit more treatment-dependent trajectories, with pronounced shifts in community composition in TP and AF_T compared to AF_C and MC. The communities of both soil and flying predators are mostly driven by temporal changes, however differences between treatments are observed, especially MC which differs from treatments with trees. In contrast, granivores and leaf feeders display erratic trajectories, indicating high variability in community composition across months.

4. Discussion

4.1. From herbivores to pest pressure

Although herbivores were overall more numerous in monocultures than in treatments with trees, the impact of trees on their population appeared to be very time- and taxon-dependent. Granivores and sap feeders exhibited lower abundance in tree-associated plots (AF_T and TP), indicating that trees may have a suppressive effect on certain herbivores, possibly via top-down regulation or resource dilution as explained by the resource concentration hypothesis (Root, 1973) (Table 2). In monocultures, high plant uniformity and density facilitate herbivore specialization and population growth. By contrast, in agroforestry, greater plant diversity may dilute host plant signals, reducing herbivore attraction and feeding efficiency (Letourneau et al., 2011). While Siemann et al. (1998) found that herbivore diversity is driven more by parasite and predator diversity than plant diversity, the links between plant and herbivore diversity appear to be complicated and highly scale and context dependent, and still need to be investigated (Moreira et al., 2016). Granivores were highly dominated by the ant genus *Messor* and the carabid genus *Harpalus (*e.g. *H. distinguendus*, *H. affinis*). Many granivorous arthropods, such as carabid beetles and harvester ants, exhibit high dispersal abilities, allowing them to exploit seed resources across multiple habitat types, potentially minimizing the impact of local habitat modifications. Moreover, granivores exhibited erratic trajectories, indicating that their community composition was highly variable across months and treatments, suggesting a stronger influence of stochastic environmental factors rather than agroforestry management. For granivores, such variability may be driven by spatial heterogeneity in seed availability, predator interactions, or weather conditions, which can influence post-dispersal seed predation rates (Blubaugh and Kaplan, 2016).

Sap feeders, particularly Thysanoptera and Aphididae, exhibited a marked increase in May across all treatments (Fig. 2A, C). These population dynamics are closely tied to crop and tree leaf development stages, as these insects rely on phloem sap and young plant tissues, which fluctuate in quality and availability throughout the growing season (Awmack and Leather, 2002; Tooker and Giron, 2020). This trend aligns with the variations in availability of nitrogen-rich plant sap in developing cereals (Tooker and Giron, 2020) and supports the plant quality hypothesis, which predicts that phytophagous insect populations peak when plant nutritional quality is highest (Awmack and Leather, 2002). While Thysanoptera peaked in MC and AF_C, Aphididae were more numerous in treatments with trees, suggesting different resource preferences. For Psylloidea (Fig. 2B), an early-season peak (March) was observed in MC and AF_C, followed by a sharp decline in April and May, which may reflect a depletion of host resources or increasing top-down control by natural enemies (Bianchi, 2022).

For the leaf feeders, abundance and diversity seemed to be very variable, with a moderate impact of treatment and trapping month. The reduction in chewer diversity in agroforestry alleys compared to monocultures in April (Fig. 3b) could reflect a pattern of resource limitation and altered plant-insect interactions. Chewing herbivores often rely on continuous access to specific host plants (Roslin et al., 2006). In agroforestry systems, tree rows may disrupt host continuity by reducing the dominance of specific crop species, and creating a more fragmented feeding landscape. This can negatively impact or delay the settlement of specialized herbivores that rely on a single plant species while potentially favoring generalist species that can exploit a wider range of plant resources. For leaf feeders, the high variability in community trajectories suggests that their populations may be influenced by episodic disturbances, such as pest outbreaks or localized predator activity. Leaf-chewing insects, including Lepidoptera and Coleoptera, are often subject to strong top-down control from predators and parasitoids, which can cause unpredictable fluctuations in abundance and diversity over time (Vidal and Murphy, 2018).

The abundance and diversity of herbivores present in treatments with trees can raise concerns about the risk of creating a reservoir of generalist herbivores that could attack the crop. However, not all herbivore species pose a risk to the crop, as not all feed on cereals. For example, Aphididae, which were abundant under trees, were widely distributed on thistles and other understory vegetation. In the same way, Psocodea, mainly consume lichens, fungi and organic debris, and possibly small amounts of leaf (Baz, 2004). Moreover, some of the herbivores collected are specialists of other weeds: their presence can then be beneficial to the crop, helping to limit the spread of weeds without herbicide treatment. This is the case, for example, of the weevil *Hypurus bertrandi* (Perris, 1852), a specialist herbivore of purslane (*Portulaca oleracea* L., 1753) (Hoffmann and Tempère, 1944). In the same way, granivores can help regulate weed seeds (Petit et al., 2017). Even if the dietary preferences of some species or taxa are known, the lack of data for most taxa, as well as the sometimes insufficiently precise level of identification (for aphids, for example), made it impossible to confidently isolate the herbivores likely to consume the cultivated cereals.

4.2. Potential of biological control

Predators, both flying and ground-dwelling, showed contrasting responses to agroforestry depending on their foraging strategy and habitat preferences. Soil-dwelling predators, including ants (Formicidae), ground beetles (Carabidae) and spiders (Araneae), were significantly more abundant in monoculture fields (MC) than in agroforestry and tree plantations (TP), but no diversity differences were found between treatments (Tables 2 and 3). This contradicts previous studies, obtained in the same geographic region, showing that ground-dwelling predators generally benefit from agroforestry systems due to increased habitat complexity and resource stability (Boinot et al., 2020, 2019). One possible explanation is that ground predators in our system responded to prey distribution patterns rather than habitat structure alone. Many ground beetles and cursorial spiders are known to disperse into open fields during peak prey availability in spring (Pardon et al., 2019), which may explain their higher abundance in MC. Alternatively, vegetation density, soil moisture and temperature fluctuations in AF-T and TP plots could have influenced predator activity levels, as tree rows often create more humid and cooler microclimates that affect ground-dwelling arthropod movement and foraging efficiency (Boinot et al., 2019; Pardon et al., 2019). However, flying predators, including flying predatory Coleoptera or Hemiptera, exhibited no significant response to treatment type, suggesting that these mobile predators may exploit resources across habitat boundaries rather than being restricted to specific plots. This is consistent with studies indicating that aerial predators are more influenced by landscape-scale habitat connectivity and prey availability than local vegetation structure (Tscharntke et al., 2007). However, similar temporal trajectories between treatments show a strong impact of phenology and climate on flying predator communities. In May, when their abundance is highest, the composition of agroforestry communities appears to be an intermediate between those in monocultures and those in tree plantations.

Parasitoids, such as Aphelinidae, Charipinae and Braconidae, were more abundant in the presence of trees compared to MC and AF_C, suggesting a favourable effect of the increased habitat complexity and resource availability in these systems (Table 2). This effect is likely due to several interacting factors. First, agroforestry plots may support greater host diversity, as trees and understory vegetation harbor alternative herbivore species that serve as hosts for parasitoids (Favor et al., 2024; Pak et al., 2015; Staton et al., 2021). Second, the complex vegetation structure in tree rows may offer shelter from extreme weather conditions, increasing parasitoid retention and population stability throughout the season (Kostenko et al., 2015; Monmany Garzia et al., 2018; Randlkofer et al., 2010). Indeed, some indirect factors of habitat structure modification –temperature, humidity and wind– are known to influence parasitoid survival and dispersal (Bouget and Duelli, 2004; Cours et al., 2023). These findings align with the enemies hypothesis (Letourneau, 1987; Root, 1973), which states that complex habitats support greater predator and parasitoid populations, thereby enhancing natural pest control.

However, the impact of agroforestry on biodiversity was more limited, as parasitoid diversity was only higher in TP compared to AF_C. This finding does not entirely support the habitat heterogeneity hypothesis that an increase in the number of different habitats leads to an increase in species diversity (MacArthur and MacArthur, 1961). In addition, the strong temporal variation of parasitoid abundance and diversity suggest that temporal availability of hosts and floral resources likely played a significant role in shaping parasitoid assemblages. Previous studies have shown that many parasitoids synchronize their life cycles with those of their hosts, particularly in agricultural landscapes where host insect populations fluctuate rapidly (Ramos Aguila et al., 2023; Welch and Harwood, 2014).

Conversely to activity-density, the lack of strong differentiation between treatments in community temporal trajectories suggests that parasitoid taxonomic richness and composition were not strongly influenced by agroforestry structures at the spatial scale examined. This could be due to their high dispersal capacity, allowing them to move freely between different habitats in search of hosts (Landis et al., 2000). This may also result from passive dispersal by wind, as trees slow wind allowing these parasitoids to settle. In our case, analyzing one of the bigger parasitoid families (Ichneumonidae), very little associations could be discovered between the crops used and the presence of certain species. The great majority of the ichneumonid species seem to be circumstantial, related to scrubs, trees or vegetation in the neighborhood. A small number of species are parasitoids of beetles like *Odontocolon quercinum* (Thomson, 1877) (hosts on oak trees) or *Phradis* (hosts on Brassicaceae) or even fungus gnats (Orthocentrinae).

Predation pressure also regulates herbivore populations through dispersal and top-down mechanisms. The observed suppression of aphid and thrips populations in tree rows (AF_T) (Fig. 2A, C) could be linked to increased predation pressure, as tree-associated plots provide stable microhabitats for natural enemies (Boinot et al., 2019; Jaworski et al., 2023). Moreover, the lower abundance of ground-dwelling predators in the tree rows in agroforestry compared to monoculture (Table 2) may reflect higher predator dispersal from tree rows into cultivated alleys during the growing season, as seen in other studies on agroforestry predator-prey dynamics (Pardon et al., 2019). Interestingly, the absence of a strong effect on predators in April (Table 2, Fig. 3) may indicate a lag in predator recruitment or temporal shifts in predation intensity (Colares et al., 2015; Fischer et al., 2022). These findings highlight the importance of maintaining spatial and temporal habitat heterogeneity to optimize biocontrol functions in agroforestry systems. Many studies consider arthropod predators and parasitoids as potential regulators of herbivores (Beizhou et al., 2011). However, not all trophic relationships are well known and, in the absence of precise information, it is difficult to estimate which of these predators and parasitoids attack herbivores directly (primary predators and parasitoids) and which consume or parasitize predators or parasitoids (secondary predators or hyperparasitoids). Furthermore, not all predators consume pests, and some may consume beneficial organisms such as detritivores, pollinators or certain herbivores. For example, crab spiders (Thomisidae), which are generalist predators, can consume pollinators, which are beneficial to crops (Camurça et al., 2024). Most of the ichneumonid wasps collected in our survey are common parasitoids of Lepidoptera (some more generalist than others, i.e. *Exetastes adpressorius* (Thunberg, 1824)*, Ichneumon sarcitorius* L., 1758 and *Ichneumon proletarius* Wesmael, 1848 but four different species from the subfamily Diplazontinae are exclusive parasitoids of hoverfly (Broad et al., 2018). Moreover, one of the most trapped species, *Cryptus bucculentus* (Tschek, 1871), has no known host records at this moment.

Thus, while most predators and parasitoids have the potential to regulate pest populations, the potential impact of some taxa may be more difficult to predict because of cascading effects. Hyperparasitism is another phenomenon that can disrupt biological control by primary parasitoids on target pests because hyperparasitoids develop at the expense of parasitoids and are therefore likely to limit control of herbivorous hosts by the next parasitoid generation (Sullivan and Völkl, 1999; Tougeron and Tena, 2019). A good example from our survey consists of species from the subfamily Charipinae (Figitidae), which are hyperparasitoids of aphids via Aphidiinae (Braconidae) and Aphelininae (Aphelinidae) and hyperparasitoids of psyllids via Encyrtidae (Menke et al., 1991).

Another difficulty in classifying taxa into trophic groups is that many species belong to more than one group, depending on their development stage or the resources available (Bianchi et al., 2022). For example, the larvae of some Syrphidae species, such as *Sphaerophoria scripta* (Linnaeus, 1758), are polyphagous predators, whereas their adults are pollinators (Gomez-Polo et al., 2014). This dietary diversity can therefore make it difficult to know whether this species has a positive, negative or neutral effect on crops. Including a large proportion of the arthropod diversity present at a site therefore gives a broader view of all the communities and dynamics at the site, but makes it more difficult to classify them into functional groups and to study the precise interactions between organisms.

4.3. Implications for pollination

Pollinators were more abundant in cultivated alleys and monocultures than in treatments with trees (TP and AF_T), especially at the end of April, when activity-density increased. This result is surprising, as trees in agroforestry systems are often thought to support pollinators by providing additional floral resources and nesting sites (Bentrup et al., 2019; Kay et al., 2020). A possible explanation is that the presence of trees and understory vegetation (comprising tall plants such as thistles) may have reduced the attractiveness of yellow pan traps, as they are less visible and also compete with many colored flowers (Vrdoljak and Samways, 2012). Additionally, many hymenopteran pollinators are affected by and may avoid tree shade. Moreover, as for many Fabaceae, the specific structure of *R. pseudoacacia* flowers can make it difficult or impossible for many generalist pollinators to pollinate them. Finally, pollinators, such as bees, are mobile and therefore affected by the distribution of resources at the landscape scale (Kremen et al., 2007). As the flowers on the site were all under and around the trees, pollinators may have been attracted by the density of flowers, but were more likely to be captured in zones where their moving activity is higher in the absence of flowers to pollinate.

While pollinator diversity showed no significant treatment effects, the temporal structuring of pollinators observed in the PCoA suggests that their community composition shifted over time, possibly reflecting variations in floral resource availability, temperature, or competition with other insect groups (Bentrup et al., 2019; Centeno-Alvarado et al., 2023; Staton et al., 2022). Community composition seemed to differ between treatments in April. The black locust trees flowered at the end of April/beginning of May, while most of the other plants on the site flowered in May. The flower resources available for pollinators were therefore different in April and May, possibly explaining the differences in community composition. Based on these results, it is difficult to conclude whether tree and understory vegetation in this agroforestry system impacts pollination. Studying pollinators using methods specifically designed for this group in an agroforestry system where the crop is a flowering plant remains necessary.

4.4. *Potential for organic matter degradation*

Consistently with previous studies, detritivores were more abundant and diverse in tree plantations compared to monocultures (Marchand et al., 2024). For detritivores, including e.g. Isopoda and Diplopoda, the accumulation of leaf litter and organic matter beneath tree rows likely enhances habitat suitability (Souty-Grosset et al., 2005). In contrast, in monocultures, frequent tillage and herbicide application reduce soil organic matter inputs and disrupt decomposer communities (Wolters and Ekschmitt, 1997). Conversely, increased organic matter availability under trees not only provides a direct resource base for detritivores but also modifies soil moisture and temperature conditions (Panozzo et al., 2022; Zignol et al., 2023). Although detritivore abundance was slightly lower in AF_T compared to TP, the higher abundance of detritivores in cultivated alleys of agroforestry than in the monoculture underscores the potential of agroforestry in promoting nutrient cycling and soil health in cropland by maintaining functional detritivore communities. Detritivores showed distinct treatment-dependent shifts (Fig. 3), suggesting that agroforestry may promote specialized decomposer assemblages. The presence of trees influenced the community structure of decomposers by increasing organic matter inputs from leaf litter, root exudates, and decaying plant material. Previous research has shown that detritivore communities are highly sensitive to variations in microhabitat conditions, such as moisture retention, litter composition, and microbial activity, all of which are modified by tree cover.

4.5. *Temporal dynamics and spatial heterogeneity*

Our study shows that agroforestry affects arthropod communities, but the effects vary significantly between trophic groups and months. Arthropod abundance shifted significantly throughout the season for most trophic groups, likely in response to plant phenology, climatic conditions and resource availability (Singer and Parmesan, 2010; Ovaskainen et al., 2013). From March to May, abundance generally increased in line with rising temperatures and the development of the crop, trees and understory vegetation, except for pollinators, which were more abundant in April, and leaf feeders, which were not significantly affected by month (Table 2). Globally, climate and phenology had the same positive effect on arthropod diversity, but to a lesser extent (Table 3). Overall, flying arthropod communities exhibited structured temporal trajectories, but with little differentiation between treatments (Fig. 3). This suggests that phenology, rather than habitat structure, is the primary driver of flying arthropod community composition in this agroecosystem. The variability in community dynamics of ground dwelling organisms suggests that other factors drive soil communities, such as soil properties, vegetation density or disturbances (Guo et al., 2019). These global trends may, however, hide specific dynamics at different taxonomic scales, such as the decline in Psylloidea abundance from April onwards, while sap-feeders globally peaked in May, or the increase in Syrphidae in May, while most of the other pollinators declined in May. Thus, it seems crucial to repeat protocols over time during the year, and especially at different stages of the crop development, to better understand the impact of agroforestry on arthropod communities. This is particularly important for quantifying pests and the potential for biological control, as pest outbreaks can be short and closely related to a developmental stage (Welch and Harwood, 2014).

Nevertheless, the type of treatment also appeared to be an important factor influencing the abundance and composition of arthropod communities. Many differences were observed between monocultures and tree plantations, confirming the impact of habitat complexity, plant diversity and disturbances such as tillage and treatments on arthropod trophic groups. As the communities present in the agroforestry rows were very similar to those in tree plantations, it indicates that the presence of tree rows in crops helped to restore favorable conditions for biodiversity within these rows, promoting ecosystem functions. The communities trapped in the middle of cultivated alleys were also very similar to those in monocultures. This suggests that in this agroforestry site, the effect of the presence of tree rows was limited and did not necessarily reach the middle of the cultivated alleys. As the alley cropping system studied was relatively young (8 years), it is possible that the zone of influence of the tree was limited and that measurements at intermediate distances from the trees (between 1 and 5 m) would have allowed a better quantification of the impact of the tree line and vegetation on the crop (D'Hervilly et al., 2022; Pardon et al., 2019). Finally, the trees will continue to grow, potentially increasing their impact, and the strong similarities between the arthropod communities of tree alleys (AF_T) and those of tree plantations (TP) offers an encouraging vision of the potential of agroforestry for biodiversity. Furthermore, since monoculture plots are smaller than agroforestry plots, the effects of monoculture crops may have been partially mitigated by the impact of adjacent habitats, thereby limiting the differences between agroforestry and monoculture plots.

4.6. *Trophic group assignment*

We are aware that the exclusion of certain groups could have some influence on the results. However, we consider the dataset to be strong enough to support our conclusions, given the high number of identified specimens and the diversity it encompasses. For instance, Diptera and Staphylinidae are composed of species with extremely varied trophic habits, which makes it difficult to assign them consistently to a single functional group. In addition, available knowledge on invertebrate trophic habits is huge, but it's still challenging to find reliable information on many taxa. This limitation is not unique to our study but reflects a broader issue in invertebrate ecology: the taxonomic and functional diversity of many groups remains too vast to be covered exhaustively within a single study (Srivathsan et al., 2023). Our objective was not to produce a full taxonomic inventory but to explore temporal patterns across functionally defined arthropod groups, for which the available level of identification was both realistic and adequate.

5. Conclusion

Our findings suggest that the studied agroforestry system has the potential to support natural pest control, pollination, organic matter decomposition and biodiversity conservation, but these effects vary across trophic groups and during crop development. While tree rows and associated understory vegetation can enhance the abundance and diversity of natural enemies, including predatory and parasitoid arthropods, their impact on herbivore populations is not uniform across all functional groups. Some herbivores, such as sap feeders and granivores, exhibited lower abundance in tree-associated plots, suggesting that agroforestry may help reduce pest pressure in some contexts. However, other groups, such as leaf feeders, pollinators, and aerial predators, showed high temporal variability, indicating that their response to tree cover may be influenced by resource fluctuations, dispersal capacity, and climatic conditions. This underlines the importance of studying the agroforestry system over several months or years, to assess its impact on biodiversity and the interactions between organisms.

To maximize the benefits of agroforestry for pest suppression and biodiversity conservation, targeted management strategies would combine three actions. First, tree rows would be maintained with understory vegetation to sustain natural enemy populations year-round. The persistence of predatory arthropods and parasitoids is critical for effective pest regulation in agroecosystems. Second, floral resource availability would be enhanced to attract parasitoids and pollinators. Many parasitoids and pollinators rely on nectar and pollen as supplementary food sources, particularly during critical periods of low host availability. Three, tree-crop spatial arrangements have to be adjusted to minimize potential trade-offs between pest suppression and crop yield. Optimizing tree spacing and alley width could help balance the benefits of pest suppression while minimizing competition for light, water, and nutrients between trees and crops. Selecting appropriate tree species that do not host key crop pests could further reduce potential negative impacts on adjacent fields.

While our study provides valuable insights into the effects of agroforestry on arthropod communities, further research is needed to refine our understanding of how these systems contribute to ecosystem service provision over the long term. First, we recommend investigating functional diversity to assess how changes in taxonomic composition translate into ecosystem service provision. Second, while our study analyzed trophic groups separately, food web approaches could help reveal key predator-prey relationships, cascading effects, and indirect interactions that drive community dynamics in agroforestry. Third, future research should integrate long-term monitoring approaches to assess how arthropod-mediated services change as agroforestry systems develop and whether adaptive management practices can enhance resilience to climate change. Finally, particular attention should be given to the long-term ecological consequences of the tree species selected, as species choice can strongly influence habitat structure, soil conditions, and trophic networks. In our case, *R. pseudoacacia*, although naturalized in Europe, is non-native and can become invasive under certain conditions, highlighting the need to balance its functional advantages with careful monitoring of its potential ecological impacts over time.

CRediT authorship contribution statement

Cyril Versavel: Investigation. **Paul Vignac:** Writing – review & editing, Investigation. **Luna Vion-Guibert:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Mickael Hedde:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Claire Marsden:** Writing – review & editing, Funding acquisition, Conceptualization. **Florine Degrune:** Writing – review & editing. **Marion Forest:** Writing – review & editing, Investigation. **Nicolas Hénon:** Writing – review & editing, Investigation. **Anne-Sophie Masson:** Writing – review & editing, Investigation, Data curation. **David Notton:** Writing – review & editing, Investigation. **Solène Orrière:** Writing – review & editing, Investigation. **Jean Trap:** Writing – review & editing. **Fons Verheyde:** Writing – review & editing, Investigation.

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used EditGPT in order to improve readability and language on the first version. After using this tool/service, the authors reviewed and edited the content as needed and take full responsibility for the content of the published article.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests. Mickael HEDDE reports financial support was provided by French National Institute for Agricultural Research INRAE. Mickael HEDDE reports a relationship with French National Institute for Agricultural Research INRAE that includes: employment and funding grants. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2025.110109.

Data availability

Data have been shared as supp mat

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