

EFFECTS OF AGROFORESTRY ON BIRDS, BATS AND SPIDERS IN EUROPE

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*« El error consintió en creer que la tierra era
nuestra cuando la verdad de las cosas es que
nosotros somos de la tierra »*

*« The mistake was in believing that the earth
belonged to us, when the truth is that we belong to
the earth »*

Nicanor Parra, Chilean physicist and poet

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ABSTRACT

Agricultural intensification, while initially boosting productivity, has led to significant environmental degradation. The widespread use of synthetic inputs and mechanization have contributed to the simplification of landscapes, leading to habitat loss, biodiversity decline, and the disruption of ecological processes. Consequently, the sustainability of farming systems has been compromised, endangering the provision of crucial ecosystem services essential for both the long-term agricultural viability and the human well-being.

Agroforestry—through the deliberate integration of trees into agricultural landscapes—emerges as a promising strategy to reconcile food production with the conservation of biodiversity and the maintenance of crucial ecosystem services. This thesis investigates the potential of silvoarable and silvopastoral systems to support the diversity of birds, bats, and spiders across a range of European agricultural contexts. **Chapters II, III, and IV** reveal distinct benefits of agroforestry systems for each group. While birds benefited from the structural heterogeneity provided by woody elements in agroforestry systems, bat activity and diversity were primarily influenced by prey and shelter availability—especially in fields with older deciduous trees and grazing livestock. Both bird and bat diversity responded positively to within-field variables. In contrast to birds and bats, spider diversity did not significantly respond to within-field features. However, spider community composition differed across habitat types, with agroforestry systems—due to their structural heterogeneity—supporting species with a range of habitat preferences. Overall, the findings from **Chapters II, III, and IV** indicate that agroforestry enhances bird and bat diversity compared to open agricultural fields. Moreover, by increasing within-field structural complexity, agroforestry systems also create habitat conditions favorable to both open- and woodland-associated bird, bat and spider species.

These studies highlight the potential benefits of agroforestry systems for supporting bird, bat, and spider communities. A broader implementation of such systems could play a crucial role in halting and reversing the dramatic biodiversity decline observed across European farmlands. The findings also emphasize the importance of considering multiple taxa and ecological traits in conservation strategies, as species respond differently to habitat structure and environmental variables. Moreover, the thesis underscores the value of maintaining a heterogeneous landscape mosaic composed of cultivated and permanent semi-natural and woody elements to maximize biodiversity.

Despite its ecological potential, the adoption of agroforestry in Europe remains limited, hindered by policy gaps, mechanization trends, and socio-economic barriers. Effective implementation will require coordinated efforts across policy, research, and practice, recognizing that biodiversity-friendly farming must occur at both field and landscape scales. These studies contribute empirical evidence that agroforestry can serve as a keystone practice in the transition toward resilient, multifunctional agricultural landscapes that integrate biodiversity conservation with productive land use.

CHAPTER I

GENERAL INTRODUCTION

Manon Edo



Agricultural intensification: a historical perspective

The global human population is continuously increasing. As of January 1st, 2025, an estimated 8.09 billion people inhabit the Earth—an increase of nearly 2 billion since the year 2000 (6.1 billion) and more than double the population of 1975 (United Nations – World population Prospects 2024). This sustained population growth has led to a significant rise in food demand, requiring strategies that enhance agricultural productivity. As a response, societies have turned to agricultural intensification. Agricultural intensification refers to “the process of increasing the use of capital, labour, and inputs (e.g., fertilizers, pesticides, machinery) relative to land area, to increase agricultural productivity” (IPBES, 2019).

Agricultural intensification has evolved considerably since the Neolithic Revolution, approximately 10,000 years ago, when human societies began to transition from nomadic lifestyles into settled farming. Early forms of intensification included practices such as crop rotation, irrigation and soil fertilization. In Europe, the use of animal-powered machinery and the implementation of the three-field system contributed to higher yields during medieval and modern periods (Crabtree, 2010). The Agricultural Revolution of the 18th and 19th centuries further advanced productivity through selective breeding, mechanization, and improved crop rotation techniques (Newell, 1973). The enclosure movement, which consolidated fragmented land into larger private holdings, also played a role in increasing farming efficiency during the 18th and 19th centuries (Pretty and Bharucha, 2014). A major leap in intensification occurred during the Green Revolution (1940s–1970s), which introduced high-yielding crop varieties, synthetic fertilizers, chemical pesticides and herbicides, as well as expansive irrigation infrastructure (Matson et al., 1997; Pingali et al., 2012; Ramankutty et al., 2018). Livestock intensification, marked by higher animal densities in farming systems, also occurred and was accompanied by increased use of pharmaceuticals and more efficient feeding practices (Ramankutty et al., 2018). These innovations, which significantly reduced labour requirements and increased yields per unit of land, were aimed at increasing profits for farmers, alleviating poverty and food insecurity (Pingali et al., 2012).

Although agricultural intensification initially led to increased productivity, it has been accompanied by considerable social and environmental impacts – and its long-term sustainability is increasingly being called into question (Pingali et al., 2012). Poverty, food insecurity, and micronutrient malnutrition remain prevalent in low-productivity regions, while both developed and developing countries increasingly face the opposite issue of overnutrition (Pretty and Bharucha, 2014). One contributing factor to persistent poverty is that technology transfer and subsidies—for mechanization, crop production, etc....—often disadvantage smallholder and women farmers (Pingali et al., 2012). Intensified agriculture has also led to significant negative environmental impacts: tools once hailed as

revolutionary, such as synthetic fertilizers and pesticides, have revealed major ecological and agronomic drawbacks. For example, in Scotland, wheat yields increased by 201% between 1967 and 1999 but began to stagnate in the 1990s despite continued high input levels (Burian et al., 2024). A similar trend occurred in France and North-America, where wheat and corn yields growth plateaued around the year 1990-2000 (Matson et al., 1997; Poux & Aubert, 2021). These cases illustrate a broader pattern: after initially supporting unprecedented gains of agricultural productivity, high-input systems were reaching a state of yield stagnation or even an increase of crop losses (Bommarco et al., 2011; Oerke, 2005). The once-promising vision of limitless productivity through intensification has increasingly come to resemble a dead end. The environmental consequences of these practices have become more apparent, leaving long-lasting degradation on agricultural land. Agricultural systems became “intensification traps”, where high input levels eventually lead to production declines due to negative feedback from biodiversity loss, soil degradation, greenhouse gas emissions, and water resource impacts (Burian et al., 2024; Ramankutty et al., 2018).

Limits of conventional agricultural intensification

Conventional agricultural intensification has historically been accompanied by a continuous expansion of croplands and pasturelands over millennia, replacing forests, grasslands, savannas and shrublands (Burian et al., 2024; Ramankutty et al., 2018). Globally, the area of croplands and pasturelands increased approximately fivefold between 1700 and 2007 — from about 3 to 15 million km² for croplands and from about 5 to 27 million km² for pastures (Ramankutty et al., 2018). This agricultural expansion resulted in the conversion of 30% of the world’s temperate and tropical forests as well as the loss of large portions of natural grasslands, savannas and shrubland (Ramankutty et al., 2018). This extensive conversion of natural ecosystems has significantly reduced the availability of productive land for further agricultural expansion (Ramankutty et al., 2018), which has thus driven an even more intensive approach to agriculture, aiming to produce greater yields per unit area within the limited available farmland (Pingali, 2012; Tilman et al., 2011). In 2001, Tilman et al. projected that, if current trends continued, “10⁹ hectares of natural ecosystems would be converted to agricultural land by 2050. This expansion would be accompanied by a 2.4- to 2.7-fold increase in nitrogen- and phosphorus-driven eutrophication across terrestrial, freshwater, and coastal marine ecosystems, along with comparable increases in pesticide use”. Numerous studies have since highlighted the severe ecological impacts of intensified agriculture on agroecosystems, including water pollution (Moss, 2008) and soil erosion (Bommarco et al., 2013). Mechanized land conversion and the heavy application of chemical inputs have contributed to the degradation of soil structure, leading to compaction, reduced organic matter, and subsequent declines in microbial biomass and soil functional stability and fertility (Bommarco et al., 2013; Loveland, 2003; Matson et al., 1997).

Additionally, "over-intensification"—marked by enlarged monoculture fields and reduced crop diversity—has resulted in the destruction of non-crop habitats and the structural simplification of ecosystems at both field and landscape scales (Benton et al., 2002 and 2003; Šálek et al., 2018; Tilman et al., 2001; Tscharntke et al., 2005). This homogenization of habitats has drastically reduced breeding, foraging, roosting, and overwintering sites for many species. Combined with the intensive use of pesticides and fertilizers, this habitat loss and conversion of natural habitats to agricultural use has driven sharp declines in farmland biodiversity, affecting plants, arthropods, birds, and mammals. (Benton et al., 2002; Donald et al., 2001; Fahrig, 2003; Kleijn et al., 2009; Mickleburgh, 2002; Pekin and Pijanowski, 2012). The loss of biodiversity poses serious risks to the functionality and stability of farmland ecosystems by undermining essential ecosystem services such as pollination and biological pest control (Matson et al., 1997; Potts et al., 2010; Tscharntke et al., 2005). Alarmingly, this decline in biodiversity and associated ecosystem services remains ongoing (Kortman et al., 2025; Sala et al., 2000; Tilman et al. 2001).

Compounding these issues, climate change, biological invasions, and habitat fragmentation of the agricultural landscape further constrain species' ability to migrate or adapt to shifting environmental conditions (Tilman et al., 2001). These converging stressors intensify biodiversity loss and may trigger feedback loops that accelerate ecosystems degradation. If these dynamics persist unchecked, they could lead to irreversible species extinctions and long-term disruptions to ecosystem functions. Humanity must confront a critical reality: the expansion of intensively managed agricultural land is no longer a sustainable solution. To meet the urgent climatic, economic, and social challenges ahead, there is a pressing need to transition toward new agricultural paradigms. A sustainable and resilient agricultural system must simultaneously maintain productivity, minimize environmental impacts, and actively conserve and restore biodiversity within agricultural landscapes (Bommarco et al., 2013; Tilman et al., 2001). This transition may be achievable through the adoption of sustainable agricultural practices that take advantage of ecological interactions within agricultural systems (Bommarco et al., 2013; MacLaren et al., 2022).

Agroforestry as a pathway for sustainable agricultural transformation

Provisioning ecosystem services—such as the production of food, fibre, and energy—are fundamentally dependent on regulating (e.g., pest control, crop pollination, erosion control, climate and water regulation), and supporting (e.g., soil formation and retention, nutrient cycling and provision of habitat and biodiversity) ecosystem services (Fagerholm et al., 2016; Millenium Ecosystem Assessment, 2005). Enhancing and restoring both regulating and supporting ecosystem services in agricultural systems offers a pathway towards reducing reliance on anthropogenic inputs and achieving sustainable, environmentally friendly crop production. This goal is shared by several approaches including

ecological intensification (Bommarco et al. 2013; MacLaren et al., 2022), agroecology (Wezel et al., 2009), sustainable intensification (Pretty and Bharucha, 2014; Helfenstein et al., 2020), and climate-smart agriculture (Lipper et al., 2014). Agroforestry, by reintroducing permanent and semi-natural habitats and increasing structural heterogeneity in farmland, aligns well with these movements and stands out as a promising solution to simultaneously address productivity and sustainability challenges (Fagerholm et al., 2016; Pantera et al., 2021).

Agroforestry involves the deliberate integration of trees or shrubs with crops and/or livestock on the same land unit, either simultaneously or sequentially (Nair, 1993). Across Europe, a variety of land management practices are encompassed within the definition of agroforestry, including forest farming, riparian buffer strips, windbreaks, orchard intercropping (e.g., *Streuobst*), silvoarable and silvopastoral systems (Nerlich et al., 2013; Rubio-Delgado et al., 2024). Silvoarable systems—where trees are planted in rows among arable crops—and silvopastoral systems, which integrate trees with livestock grazing and forage production, represent key agroforestry models in Europe, particularly noted for their high level of spatial integration of trees directly within agricultural fields (Nerlich et al., 2013).

By increasing structural complexity and landscape heterogeneity, agroforestry systems can foster beneficial ecological and economic interactions among their components—provided they are well-designed and appropriately managed by farmers (Mosquera-Losada et al., 2008). Agroforestry is not a new concept; it has deep historical roots in Europe and was much more widespread in the past (Nerlich et al., 2013). During the Neolithic period, woodland pastures and silvopastoral systems were common in several regions (Nerlich et al., 2013). Agriculture and forestry were interlinked: tree fodder, litter collected in woodlands as well as ash and manure played key roles in nutrient transfers from woodlands to cultivated fields (Smith 2010). Traditional systems such as *Dehesas* and *Montados* in Spain and Portugal, which integrate oak woodlands with extensive livestock grazing, exemplify long-standing agroforestry systems that have transformed otherwise marginal Mediterranean landscapes into productive land for over 4,500 years (Joffre et al. 1999). Similarly, hedgerows and windbreaks, once widespread in the Atlantic and Central European regions, served as field boundaries, while *Streuobst* (or *pré-vergers*) systems in France and Germany integrated diverse fruit tree varieties with cropland or pasture (Herzog, 1998; Nerlich et al., 2013). However, these systems declined significantly with the rise of agricultural intensification. Especially in the 20th century, the shift toward mechanized, large-scale monocultures rendered trees and hedges as obstacles to efficiency. The introduction of chemical fertilizers and crop rotation further reduced agriculture's dependence on nutrient transfers from woodlands, driving both a spatial and functional separation between agricultural and forested lands (Nerlich et al., 2013). This divide has been further entrenched by the development of distinct and often disconnected policies governing forests and agriculture (Fagerholm et al., 2016).

With growing awareness of the limitations of conventional intensification and its environmental consequences, agroforestry is now regaining attention for its multifunctional benefits. These systems

offer the potential to simultaneously enhance agricultural productivity and provide crucial ecological, socio-economic and cultural services (Fagerholm et al., 2016; Mosquera-Losada et al., 2008). Economically, agroforestry allows for the diversification of farm outputs—such as food, fodder, and timber—thereby improving farmer income stability and resilience. Notably, the integration of trees and crops can even outperform tree plantations and monocultures in overall productivity (Graves et al., 2007), due to the complementary use of resources by the trees and crops. The biophysical interactions between the woody and non-woody components support key supporting and regulating ecosystem services (Jose, 2009), including improved water retention (Joffre and Rambal, 1988), enhanced nutrient cycling, increased carbon sequestration and soil organic matter (Fernández-Núñez et al., 2010; Jose, 2009; Nair et al., 2009;) as well as reduced soil erosion, nutrient leaching and windspeed (Torralba et al., 2016; Palma et al., 2007). Agroforestry systems have been shown to support the diversity of a wide range of taxa, including birds (McAdam et al., 2007; Mupepele et al., 2021), bats and small mammals (Klaa et al., 2005) as well as arthropods (Pardon et al., 2019) such as spiders (Boinot et al., 2019). These species benefit from the diverse habitats provided by trees and hedgerows, which offer foraging, shelter, breeding, and overwintering opportunities. In turn, increased biodiversity enhances other key ecosystem services such as pest regulation and pollination (Boinot et al., 2019; Staton et al., 2019; Varah et al., 2013), thereby reinforcing agricultural sustainability. Altogether, a growing body of evidence supports the potential of agroforestry as an ecologically and economically viable approach to sustainable land management.

Effect of silvoarable and silvopastoral agroforestry on birds, bats and spiders: addressing the lack of European-scale studies

Although the ecological benefits of silvoarable and silvopastoral systems have been investigated for certain taxa, most existing studies are region-specific, with a notable lack of research conducted at a European scale. Yet, large-scale insights are essential if agroforestry is to be effectively integrated into continent-wide agricultural and conservation policies. In particular, silvoarable and silvopastoral systems—where trees are closely interwoven within crop and pasture areas—present unique ecological dynamics that differ from edge-based tree plantings (Nerlich et al., 2013). These systems therefore warrant dedicated, large-scale studies to fully understand their biodiversity contributions and to inform targeted agroforestry strategies across diverse European landscapes. Data remain scarce regarding the impacts of silvoarable and silvopastoral systems on key functional taxa such as birds, bats, and ground-dwelling spiders. These groups contribute significantly to natural pest control in agricultural systems but have suffered substantial population declines in recent decades, largely due to agricultural intensification and landscape simplification. Their sensitivity to environmental change underscores the urgent need to evaluate their responses to alternative land-use strategies, such as agroforestry, in order to halt and potentially reverse their diversity loss in farmland ecosystems.

This thesis aims to address existing knowledge gaps by providing empirical data from diverse regions across Europe. It allows to better understand the effect of silvoarable and silvopastoral systems on the abundance, alpha and beta diversity and community structure of birds (**Chapter II**), bats (**Chapter III**), and spiders (**Chapter IV**) in European farmland. To our knowledge, this research represents the first study which examines the effects of mature European silvoarable and silvopastoral systems on birds, bats, and spiders across multiple countries.

Chapter II investigates the capacity of agroforestry systems to support bird diversity compared to open agricultural land, forests and orchards, with a comparative approach between Mediterranean and temperate regions. **Chapter III** explores the effects of silvoarable versus silvopastoral systems on bats via the measure of bat activity. The influence of tree characteristics such as tree type (deciduous vs. coniferous) and tree age on bat activity are also addressed in **Chapter III**. **Chapter IV** focuses on ground-dwelling spiders, evaluating how different land use types and field size shape their community composition and diversity. In **Chapters III and IV**, bat activity and spider diversity were analysed and compared across different land-use types, including silvoarable and silvopastoral systems, as well as reference habitats such as pastures, croplands, forests, and orchards. The research draws upon field data, collected from nine sites across eight European countries, offering a robust foundation for evaluating the pan-European relevance of agroforestry for biodiversity conservation. In **Chapter III**, data were collected from 65 fields (hereafter referred as “plots”) across 8 sites in Germany, Switzerland, France (two sites), England, Italy, Spain, and Portugal.

In **Chapter V**, the localized responses of birds, bats, and spiders to agroforestry systems—investigated in **Chapters II, III, and IV**—are integrated into a broader multi-taxa and landscape-level perspective. This synthesis contributes to a more comprehensive understanding of how agroforestry systems can support biodiversity across European agricultural landscapes. The findings of this thesis will help to inform and support evidence-based policymaking, thereby contributing to the development of sustainable agricultural strategies throughout Europe.

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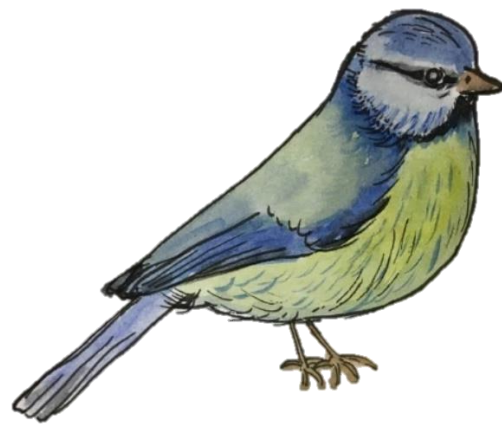
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CHAPTER II

AGROFORESTRY SUPPORTS HIGH BIRD DIVERSITY IN EUROPEAN FARMLAND

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Agroforestry supports high bird diversity in European farmland

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Abstract

Intensification and homogenization of agricultural landscapes have led to a strong decline in European farmland birds. Agroforestry systems, which were widespread in the past, are regaining attention as they could return structural heterogeneity to agricultural landscapes. However, few studies focus on the effects of such systems on biodiversity and especially bird diversity. We hypothesized that agroforestry systems host a higher alpha and beta diversity of birds compared to open agriculture as well as distinct bird communities. Moreover, we expected that bird communities in temperate Europe and the Mediterranean are differently affected by agroforestry systems. In this study, we assessed breeding bird diversity via audio recordings in nineteen mature agroforestry plots, comprising both silvoarable and silvopastoral systems distributed across seven countries in temperate and Mediterranean Europe. For comparison, bird diversity was also assessed in nearby open agricultural land, forests, and orchards. Bird species richness in agroforestry was more than doubled compared to open agricultural land and similar to the diversity found in forests and orchards. Community composition and within-habitat beta diversity differed between the habitat types and between European regions. While temperate agroforestry systems hosted generalist and woody habitat species, bird communities in Mediterranean agroforestry were composed of species from both open and woody habitats. Beta diversity was significantly higher in agroforestry than in open agriculture in temperate systems but not in the Mediterranean. Our study demonstrates that agroforestry systems represent a valuable habitat for breeding birds in European agricultural landscapes. A wider adoption of these systems could thus contribute to halting and reversing the decline in bird diversity, especially in temperate agricultural landscapes.

Keywords Agriculture · Biodiversity · Community composition · Europe · Silvoarable systems · Silvopastoral systems

1 Introduction

Across Europe, farmland biodiversity has been declining markedly over the last decades (Benton et al. 2002; Donald et al. 2001). The main reason for the decline is agricultural intensification, which started in the second half of the twentieth century, aiming to increase agricultural yields (Pain and Pienkowski 1997; Tschardt et al. 2005). Consequences that arose from changes in farming practices are numerous,

including an increase in field sizes, often associated with a reduction of semi-natural and edge habitats, higher stocking densities, a reduction of crop diversity, and an increased use of agrochemicals and pesticides (Newton 2004; Pain and Pienkowski 1997; Robinson and Sutherland 2002; Stoate et al. 2001). This led to a considerable loss of heterogeneity at both field and landscape scales resulting in habitat loss for many taxa including birds (Benton et al. 2002; Donald et al. 2006; Voříšek et al. 2010; Kamp et al. 2021). As the global demand for agricultural products will continue to increase during the twenty-first century (Tilman et al. 2011), there is an urgent need to identify and implement food production systems that maintain and restore biodiversity (Bommarco et al. 2013).

In contrast to intensified open farmland, agroforestry systems provide a high structural heterogeneity and incorporate woody plants. Agroforestry exists in a remarkable diversity all over Europe but was much more widespread in the past (Nerlich et al. 2013). In agroforestry, trees and shrubs are

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deliberately combined with crops and/or livestock on the same land (Fig. 1) (Nair 1993). Benefits can be both ecological and economic, resulting from interactions between the woody and non-woody components (Mosquera-Losada et al. 2009, <http://apps.fao.org/>). An example in temperate Europe are the so-called *Streuobstwiesen*, i.e., orchards combining fruit trees with either cropland, meadows, or pastures (Herzog 1998). In the Iberian Peninsula, there are the savannah-like *dehesas* (Spain) and *montados* (Portugal), in which oak-grassland ecosystems have been shaped by centuries of pastoralism and human management (Joffre et al. 1999). These systems support high biodiversity and are culturally significant (Moreno and Pulido 2009; Moreno et al. 2018). By (re-)integrating structural heterogeneity into agricultural landscapes, agroforestry systems have the potential to be part of a more resilient and sustainable agriculture. Providing a compromise between production demands and nature conservation needs, these systems have recently regained attention (Jose 2009; Quinkenstein et al. 2009; Nerlich et al. 2013).

In agroforestry systems, productivity can be increased compared to arable cropland and woodland systems managed separately through the complementary use of light, nutrients, and water as well as the production of different goods, e.g., forage, wood products, fodder, crops, and livestock (Cannell et al. 1996; Graves et al. 2007). Additionally, agroforestry systems support a wide variety of ecosystem services (Fagerholm et al. 2016; Jose 2009) such as carbon storage (Nair et al. 2009), reduction of soil erosion and leaching of nutrients, and improvement of soil fertility and nutrient cycling (Nair 2007; Torralba et al. 2016) as well as water retention (Joffre and Rambal 1988). Due to their high internal heterogeneity, agroforestry systems offer a diversity of food resources and habitat structures (McArthur 1958) and have thus also been found to support biodiversity (Jose 2009; McAdam and McEvoy 2009; Torralba et al. 2016). However, only a few studies focused on the effects of

European agroforestry systems on bird diversity (McAdam et al. 2007; Mupepele et al. 2021). Many bird species in farmland depend on the presence of trees and shrubs (Jakobsson and Lindborg 2017; Rösch et al. 2023). Thus, the benefits of agroforestry on birds can be expected to be strong. In contrast to annual crops, agroforestry systems are passing through different stages of tree maturity over decades. These stages may be preferred by different species of birds, similar to the successional stages of forests (Helle and Mönkkönen 1985). Thus, a higher turnover of bird species (β diversity) can be expected among agroforestry systems than among open farmland. Other studies have dealt with wood pastures (a type of silvopasture) and showed that bird diversity was higher in wood pastures compared to open pastures (Hartel et al. 2014; Morgan-Davies et al. 2008). However, the studied wood pastures served mostly for conservation management in forested areas and not for food production in agricultural landscapes, on which we focus in the current study.

Our objective was to compare breeding bird diversity of agroforestry with purely woody and agricultural reference areas. We used acoustic recording on eight agroforestry sites comprising nineteen mature agroforestry plots across seven countries in temperate and Mediterranean Europe.

Specifically, we tested the following hypotheses: (1) Due to a high structural heterogeneity provided by the presence of trees, bird species richness is higher in agroforestry systems compared to open agriculture and similar to bird richness in orchards and forests. (2) European agroforestry systems, with their combination of trees and open vegetation, support distinct bird communities composed of species from both open and woody habitats. (3) Due to the variety of agroforestry systems across Europe and their variation in tree maturity, their β diversity is higher than in open agriculture. (4) Due to differences in the structure of forests and open agricultural land, the effects of agroforestry on bird diversity differ between temperate Europe and the Mediterranean.

Fig. 1 **a** A silvopastoral site with holm oak and cattle-grazed pastures in the *dehesas* of Extremadura, Spain. **b** A silvoarable site with apple trees and strawberries near Sursee, Switzerland.



2 Material and methods

2.1 Study sites

The study was carried out in eight different agroforestry sites with either silvoarable (combination of trees and crops) or silvopastoral systems (combination of trees and livestock) and nearby control plots. The sites were located in seven countries across temperate Europe (England, Switzerland, Central France, Germany; hereafter “temperate sites”) and Southern Europe (Southern France, Italy, Portugal, and Spain; hereafter “Mediterranean sites”).

In each site, one to three agroforestry plots with mature trees (at least 15 years old) were selected. Reference areas were chosen to contain the same woody and agricultural component as the agroforestry system. Thus, open pastures served as a reference for silvopastoral systems and cropland for silvoarable systems. For the woody component, we used forest as a reference area, and added orchards as a reference where the tree component of agroforestry was fruit or nut trees. Forests were selected according to the following definition “land with tree cover or equivalent stocking level of more than 10% and with an area of more than 0.5 hectares” (FAO, <http://apps.fao.org/>). Moreover, in this study, the control plots defined as forests contained two or more different tree species with part of the trees aged more than 30 years. Conversely, in orchards, i.e., fruit or nut-producing orchards, only trees of the same species and of similar age as in the respective agroforestry plot were present.

In the temperate sites, agroforestry plots, forests, and orchards were dominated by broad-leaved trees. In the Mediterranean sites, tree stands consisted of walnuts, oaks, or pines. The agroforestry sites in England, Switzerland, and Southern France were silvoarable systems with trees aged 24, 14, and 27 years, respectively. Silvopastoral sites contained trees aged 20 (Germany), 35 (Central France), 90 (Italy), 25 (Portugal), and 175 (Spain) years. The agroforestry and reference plots were always located in the same region (see Table S1), to minimize the variation of, e.g., climate, soil, and the surrounding landscape. A total of nineteen agroforestry plots (six silvoarable and thirteen silvopastoral plots), eighteen open agricultural plots, fifteen forests, and eight orchards were sampled. The geographic location of the study sites is shown in Fig. 2. Detailed characteristics of the sampled silvoarable and silvopastoral agroforestry plots as well as the associated control plots are summarized in Table S1.

2.2 Data collection

Bird diversity was assessed using autonomous sound recorders (AudioMoth V1.1.0, Open Acoustic Devices, firmware version 1.7., configuration app version 1.6.0).

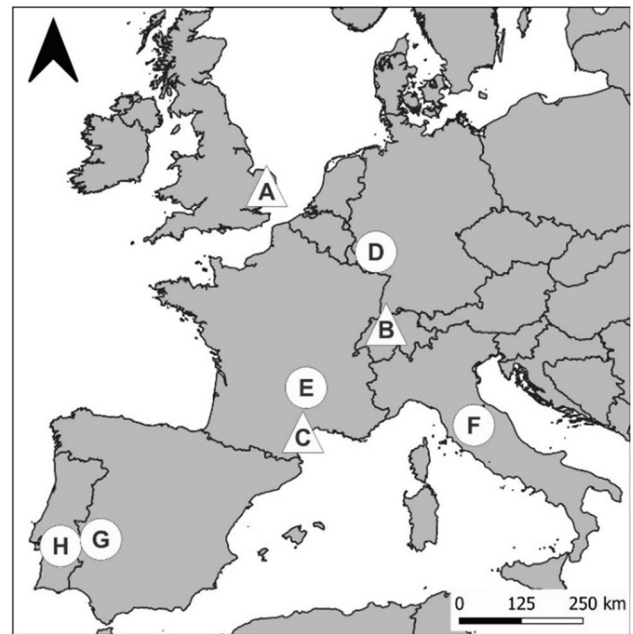


Fig. 2 Geographic location of the study sites. triangles = silvoarable systems, circles = silvopastoral systems, A = Wakelyns (UK), B = Sursee (CH), C = Restinclières (FR), D = Bannmühle (DE), E = Lamartine (FR), F = Tenuta di Paganico (IT), G = Dehesa de Majadas (ES), H = Moinhos de Vento (PO).

They were set up three times over the course of the breeding season (between March and July) in 2021 (England, Germany, Switzerland, and Central France) and 2022 (Southern France, Italy, Portugal, and Spain, see Table S1 for the detailed sampling dates). On each sampling date, one AudioMoth was set up in each plot, at least 20 m from the plot's edge, with a microphone oriented towards the plot's center. AudioMoths were wrapped in a single layer of clingfilm to protect them from humidity and dust. They were attached to a pole of a smaller diameter than the AudioMoths, 1.5 m above the ground. Surveys were conducted only during calm and dry weather, as bird activity can be strongly reduced by wind or rain (Bibby et al 2000; Pijanowski et al. 2011). During each of the three samplings, the AudioMoths were programmed to record continuously from 1 h before sunrise until 2 h after sunrise. To reduce possible hardware bias, recorders were rotated between plots after each sampling. Devices were programmed to record with a sampling rate of 192 kHz, a medium gain, a recording duration of 59 min and 55 s, and a sleep duration of 5 s. Recordings were saved as .wav files and stored on memory cards (SanDisk Corporation, Milpitas, CA, USA). Information about plots, their management and characteristics, and environmental parameters as well as the sampling dates were collected through a sampling sheet.

2.3 Species identification

Prior to analyses, all audio recordings were resampled at 22050 Hz, the conventional sampling rate for audible sounds (Gibbs et al. 2016) in order to improve frequency resolution.

For each plot and each of the three sampling dates, we analyzed two 10-min recordings: the first one starting at sunrise, the second starting 1 h after sunrise, since this falls within the highest singing activity of breeding birds (Bibby et al. 2000). Thus, in total 60 min were analyzed per plot. All species present in the recordings were identified aurally and visually with the help of the software Audacity® (version 5.4.8) with a 1024-point Hann window spectrogram, showing frequency variations over time. The databases Xeno-canto (www.xeno-canto.org), e-bird (www.ebird.org), and Tierstimmenarchiv (www.tierstimmenarchiv.de) were used to verify species identifications. Species that cannot be safely distinguished from closely related ones based on their songs or calls were identified to genus level, in our case *Passer* sp. and *Galerida* sp.

In each recording, all species identified by their call or song (hereafter “vocalization”) were annotated using Audacity. For each bird individual, the duration in seconds of its vocalization (maximum of 600 s) was measured. In addition, the maximal relative sound level (RSL) measured in decibels (dB) and its associated frequency in Hertz were measured using the software Kaleidoscope Pro (version 5.4.8; Wildlife Acoustics Inc., Concord, MA, USA). The parameters used were an FFT (fast Fourier transform) size of 512 and a win size of 128 in an overlapping Hann window. The RSL was measured by selecting the area around the loudest vocalization in the recording and was used as an indicator for the distance of the vocalizing individuals from the recorder (Yip et al. 2017). In the case of two individuals from the same species singing simultaneously (in 8 cases or 2.22% of the –30dB vocalization dataset (see below)), both were assessed to better represent the total species abundance. All vocalizations shorter than 5 s were removed from the dataset (short calls, probably not being territorial vocalizations) as well as aquatic species that were not associated with the study plots but with ponds located nearby. Vocalizations were included only above –30 dB, since this is the loudness typically shown by species singing within 20 m of the recorder (Manon Edo, unpublished data). This way, we made sure that the analyzed species were mostly associated with the habitat type in which the AudioMoth was located. Birds can be detected with AudioMoths over several hundred meters distance, which could have been far outside the focal habitat in many cases. Thus, the use of a minimum loudness was an important step, although it reduced the number of analyzed bird vocalizations by 75%, eliminating some species from the dataset (e.g., skylark, swallows) that were singing or calling outside the study plot.

2.4 Statistical analysis

To compare the bird diversity between the four different habitat types, different diversity indices and statistical analyses were used. In order to analyze bird species richness, we fitted mixed-effects models (R package lme4, function lmer, Bates et al. 2015) with habitat type and climate zone (temperate/Mediterranean) as explanatory variables (equation: $\text{lmer}(\text{SpR} \sim \text{Habitat} + \text{Climatic Zone} + (1|\text{Site}))$). Due to the nested design of the study, “Site” was used as a random factor. A post hoc test was used to determine pairwise differences between habitats (R package emmeans, function emmeans, Lenth 2022). Due to strong correlations between bird species richness, the number of recorded individuals, and singing activity in seconds, all analyses are based on species richness alone. To optimize the sample size, silvoarable and silvopastoral plots were analyzed together. A separate analysis of the species richness between the different habitat types for silvoarable versus silvopastoral sites is found in Supplementary Fig. S3; species richness showed the same trend between habitats for both types of systems. Bird community composition was analyzed using partial redundancy analyses (RDAs) based on the number of recorded individuals per species over the season with habitat as an explanatory variable and country as a 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, thereby giving lower weights to rare species (Legendre and Gallagher 2001). Due to strong differences in species composition, the Mediterranean sites and the temperate sites were analyzed separately. A permutation test with 9999 permutations was used to determine the significance of the results (R package vegan, function permutest, Oksanen et al. 2013). Finally, species turnover (β diversity) among habitats of the same type was assessed based on Euclidean distances for Mediterranean and temperate sites, respectively (R package vegan, functions vegdist and betadisper, Oksanen et al. 2013). The similarity of composition was calculated as distance to centroid and was compared between habitat types. Statistical significance was assessed through a permutation test with 9999 permutations (R package vegan, function permutest, Oksanen et al. 2013).

For all statistical tests, p -values lower than 0.05 were considered significant. P -values, means, and standard errors of mean ($\pm$ SE) are given in text and tables. All statistical analyses were conducted in R version 4.2.2 (R Core Team 2022). Information about species habitat specialization (Open, Forest, or Generalist) indicated in Table 1 were found at <https://www.iucnredlist.org/en>. Species categorized as “Open habitat species” are breeding in “arable land,” “grassland,” or “pastureland,” but not forest. “Forests species” are those breeding in “forest,” but none of the mentioned open habitat types. As an exception, species with forest as breeding

Table 1 Relative density, i.e., the number of vocalizing individuals summed over the three sampling dates per bird species (mean $\pm$ standard error) in open agriculture, agroforestry, forest, and orchard; letters show significant pairwise differences ($p < 0.05$) between habitats derived from post hoc tests for the respective species (bold). For each species, habitat specialization (Forest, Open, Generalist) is given the following information found on <https://www.iucnredlist.org/en>. For details about classification, see Section 2. Boldface entries all indicate significant differences.

Species	Open agriculture	Agroforestry	Forest	Orchard	Habitat
<i>Alectoris rufa</i>	0.11 $\pm$ 0.11	0 $\pm$ 0	0 $\pm$ 0	0.12 $\pm$ 0.12	Open
<i>Anthus campestris</i>	0 $\pm$ 0	0.05 $\pm$ 0.05	0 $\pm$ 0	0 $\pm$ 0	Open
<i>Anthus trivialis</i>	0.17 $\pm$ 0.17	0.05 $\pm$ 0.05	0 $\pm$ 0	0 $\pm$ 0	Generalist
<i>Carduelis carduelis</i>	0.06 $\pm$ 0.06	0 $\pm$ 0	0.07 $\pm$ 0.07	0 $\pm$ 0	Generalist
<i>Certhia brachydactyla</i>	0 $\pm$ 0	0.32 $\pm$ 0.22	0.27 $\pm$ 0.12	0 $\pm$ 0	Forest
<i>Cettia cetti</i>	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0	0.12 $\pm$ 0.12	Other
<i>Chloris chloris</i>	0 $\pm$ 0	0.11 $\pm$ 0.11	0.07 $\pm$ 0.07	0 $\pm$ 0	Generalist
<i>Clamator glandarius</i>	0 $\pm$ 0	0.05 $\pm$ 0.05	0 $\pm$ 0	0 $\pm$ 0	Open
<i>Columba palumbus</i>	0 $\pm$ 0	0 $\pm$ 0	0.13 $\pm$ 0.09	0.12 $\pm$ 0.12	Generalist
<i>Corvus corone</i>	0 $\pm$ 0 b	0 $\pm$ 0 b	0 $\pm$ 0 b	0.25 $\pm$ 0.16 a	Generalist
<i>Cuculus canorus</i>	0 $\pm$ 0	0 $\pm$ 0	0.07 $\pm$ 0.07	0 $\pm$ 0	Generalist
<i>Curruca communis</i>	0.06 $\pm$ 0.06	0.05 $\pm$ 0.05	0 $\pm$ 0	0 $\pm$ 0	Open
<i>Curruca melanocephala</i>	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0	0.12 $\pm$ 0.12	Generalist
<i>Cyanistes caeruleus</i>	0 $\pm$ 0	0.47 $\pm$ 0.19	0.27 $\pm$ 0.15	0.12 $\pm$ 0.12	Forest
<i>Cyanopica cooki</i>	0.06 $\pm$ 0.06	0.05 $\pm$ 0.05	0 $\pm$ 0	0 $\pm$ 0	Forest
<i>Dendrocopos major</i>	0 $\pm$ 0	0.05 $\pm$ 0.05	0.13 $\pm$ 0.13	0 $\pm$ 0	Forest
<i>Dendrocoptes medius</i>	0 $\pm$ 0	0 $\pm$ 0	0.07 $\pm$ 0.07	0 $\pm$ 0	Forest
<i>Emberiza calandra</i>	0.56 $\pm$ 0.28	0.26 $\pm$ 0.15	0.27 $\pm$ 0.21	0 $\pm$ 0	Open
<i>Erithacus rubecula</i>	0 $\pm$ 0 a	0.21 $\pm$ 0.12 ab	0.73 $\pm$ 0.37 b	0.12 $\pm$ 0.12 ab	Generalist
<i>Falco tinnunculus</i>	0 $\pm$ 0	0.05 $\pm$ 0.05	0 $\pm$ 0	0 $\pm$ 0	Generalist
<i>Fringilla coelebs</i>	0.06 $\pm$ 0.06 a	1.05 $\pm$ 0.38 ab	1.53 $\pm$ 0.56 b	0.12 $\pm$ 0.12 ab	Forest
<i>Galerida sp.</i>	0.33 $\pm$ 0.2	0.16 $\pm$ 0.12	0 $\pm$ 0	0.12 $\pm$ 0.12	Open
<i>Garrulus glandarius</i>	0 $\pm$ 0	0 $\pm$ 0	0.13 $\pm$ 0.09	0 $\pm$ 0	Forest
<i>Lophophanes cristatus</i>	0 $\pm$ 0	0 $\pm$ 0	0.07 $\pm$ 0.07	0 $\pm$ 0	Forest
<i>Lullula arborea</i>	0 $\pm$ 0	0.05 $\pm$ 0.05	0.13 $\pm$ 0.13	0 $\pm$ 0	Generalist
<i>Luscinia megarhynchos</i>	0.06 $\pm$ 0.06	0.21 $\pm$ 0.21	0.27 $\pm$ 0.21	0.38 $\pm$ 0.26	Forest
<i>Milvus milvus</i>	0 $\pm$ 0	0.05 $\pm$ 0.05	0 $\pm$ 0	0 $\pm$ 0	Forest
<i>Motacilla alba</i>	0 $\pm$ 0	0.05 $\pm$ 0.05	0 $\pm$ 0	0 $\pm$ 0	Open
<i>Muscicapa striata</i>	0 $\pm$ 0	0 $\pm$ 0	0.07 $\pm$ 0.07	0 $\pm$ 0	Generalist
<i>Oriolus oriolus</i>	0 $\pm$ 0	0.11 $\pm$ 0.07	0.33 $\pm$ 0.27	0 $\pm$ 0	Forest
<i>Parus major</i>	0 $\pm$ 0	0.63 $\pm$ 0.28	0.4 $\pm$ 0.16	0 $\pm$ 0	Forest
<i>Passer sp.</i>	0.06 $\pm$ 0.06	0.05 $\pm$ 0.05	0 $\pm$ 0	0 $\pm$ 0	Generalist
<i>Phasianus colchicus</i>	0 $\pm$ 0	0.05 $\pm$ 0.05	0 $\pm$ 0	0 $\pm$ 0	Generalist
<i>Phylloscopus bonelli</i>	0 $\pm$ 0	0.05 $\pm$ 0.05	0 $\pm$ 0	0 $\pm$ 0	Forest
<i>Phylloscopus collybita</i>	0 $\pm$ 0 b	0 $\pm$ 0 b	0.2 $\pm$ 0.11 a	0 $\pm$ 0 ab	Forest
<i>Phylloscopus trochilus</i>	0 $\pm$ 0	0.16 $\pm$ 0.16	0 $\pm$ 0	0 $\pm$ 0	Forest
<i>Pica pica</i>	0 $\pm$ 0	0.05 $\pm$ 0.05	0.07 $\pm$ 0.07	0 $\pm$ 0	Generalist
<i>Picus viridis</i>	0 $\pm$ 0 b	0.11 $\pm$ 0.07 ab	0.33 $\pm$ 0.16 a	0 $\pm$ 0 ab	Generalist
<i>Serinus serinus</i>	0 $\pm$ 0	0.05 $\pm$ 0.05	0.33 $\pm$ 0.27	0.12 $\pm$ 0.12	Generalist
<i>Sitta europaea</i>	0 $\pm$ 0	0 $\pm$ 0	0.13 $\pm$ 0.13	0 $\pm$ 0	Forest
<i>Sturnus unicolor</i>	0.11 $\pm$ 0.08	0.26 $\pm$ 0.17	0 $\pm$ 0	0 $\pm$ 0	Generalist
<i>Sturnus vulgaris</i>	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0	0.12 $\pm$ 0.12	Generalist
<i>Sylvia atricapilla</i>	0 $\pm$ 0 b	0.37 $\pm$ 0.23 b	1.2 $\pm$ 0.33 a	0.12 $\pm$ 0.12 b	Forest
<i>Sylvia borin</i>	0 $\pm$ 0	0.05 $\pm$ 0.05	0 $\pm$ 0	0 $\pm$ 0	Forest
<i>Troglodytes troglodytes</i>	0 $\pm$ 0 a	0.21 $\pm$ 0.12 ab	0.87 $\pm$ 0.47 b	0 $\pm$ 0 ab	Forest
<i>Turdus merula</i>	0.06 $\pm$ 0.06	0.37 $\pm$ 0.17	0.8 $\pm$ 0.38	0.38 $\pm$ 0.18	Forest
<i>Turdus philomelos</i>	0 $\pm$ 0	0.11 $\pm$ 0.11	0.27 $\pm$ 0.12	0.12 $\pm$ 0.12	Forest
<i>Turdus viscivorus</i>	0.06 $\pm$ 0.06	0.05 $\pm$ 0.05	0.13 $\pm$ 0.09	0 $\pm$ 0	Forest
Mean per habitat	1.72 $\pm$ 0.54 a	6 $\pm$ 1.11 bc	9.33 $\pm$ 1.26 c	2.5 $\pm$ 0.87 ab	

habitat of “major importance” were classified as forest species even if open habitats were listed for breeding, as well (e.g., the common chaffinch, *Fringilla coelebs*). Species categorized as “Generalist” are those associated with “forest” AND “arable land,” “grassland,” or “pastureland.” One species with neither forest, arable, or pastureland as breeding habitat is categorized as “other.”

3 Results

3.1 Species richness

In total, 48 different bird species were recorded (Table 1). Fourteen species were recorded in England, 16 in Germany, 8 in Switzerland, 19 in Central France, 13 in Southern France, 7 in Italy, 22 in Spain, and 8 in Portugal. In the temperate sites, the most common species were blackcap *Sylvia atricapilla*, common blackbird *Turdus merula*, wren *Troglodytes troglodytes*, robin *Erithacus rubecula*, and common chaffinch *Fringilla coelebs*. In the Mediterranean sites, common chaffinch *Fringilla coelebs*, corn bunting *Emberiza calandra*, nightingale *Luscinia megarhynchos*, crested or thekla lark *Galerida sp.*, and short-toed treecreeper *Certhia brachydactyla* were the most commonly found species. The total number of species varied between habitats, with 34 species recorded in agroforestry, 28 in forests, 15 in orchards, and 13 in open agriculture.

The highest bird species richness per site was recorded in forests (5.20 ± 0.51), followed by agroforestry (3.63 ± 0.53), orchards (2.38 ± 0.78), and open agriculture (1.06 ± 0.31) (Fig. 3). Bird species richness in forests and agroforestry was significantly higher than in open agriculture. Moreover, species richness in forests was significantly higher than in orchards (Fig. 3, Table S2).

3.2 Community composition

The four habitat types had distinct bird communities in both temperate and Mediterranean Europe. However, in the temperate sites, the bird communities of the different habitats were more clearly separated from each other than in the Mediterranean (Fig. 4a, b). Across both climate zones, generalist (occurring in a wide range of habitats, defined here as species breeding in forest and arable or pastureland) and forest species were associated with both agroforestry and forests, e.g., chaffinch *Fringilla coelebs*, blackbird *Turdus merula*, and great and blue tit *Parus major* and *Cyanistes caeruleus*. In temperate Europe, typical species of woodland areas such as wren *Troglodytes troglodytes* and blackcap *Sylvia atricapilla* as well as generalist species, e.g., green woodpecker *Picus viridis* and robin *Erithacus rubecula* were found in both forests and agroforestry. Only few

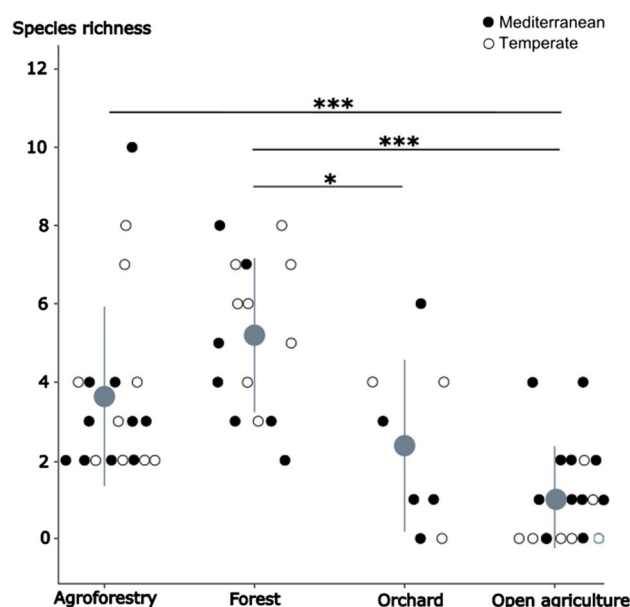


Fig. 3 Bird species richness in agroforestry ($n = 19$), forest ($n = 15$), orchard ($n = 8$), and open agriculture (cropland/pasture) ($n = 18$). Significance levels: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. See Table S2 for the detailed results of species richness in the different habitats as well as the results of mixed-effect models and post hoc tests used to determine the pairwise differences between habitats.

species and individuals (blackbird *Turdus merula*, chaffinch *Fringilla coelebs*, blue tit *Cyanistes caeruleus*, and wood pigeon *Columba palumbus*) were observed in temperate orchards and open agriculture. In the Mediterranean, forest species such as golden oriole *Oriolus oriolus* and short-toed treecreeper *Certhia brachydactyla* were common in both agroforestry and forest. Species typical for open or semi-open areas such as corn-bunting *Emberiza calandra*, *Galerida sp.* larks, and spotless starling *Sturnus unicolor* were present in both open agriculture and agroforestry of the Iberian Peninsula. The corn-bunting *Emberiza calandra* was also present in the Spanish forests and larks *Galerida sp.* in the Portuguese pine orchards. The European serin *Serinus serinus*, a generalist species, was recorded in Mediterranean agroforestry and forest plots.

3.3 β diversity within habitat types

In temperate Europe and the Mediterranean, β diversity (average distance to centroid) was significantly higher among forest plots than among open agriculture and orchards (Fig. 5a, b). Moreover, in temperate Europe, β diversity was significantly higher among agroforestry than among open agriculture. The low distances to centroid in temperate open agriculture and to a lesser extent in orchards are probably largely due to the low species richness (Fig. 3), with those habitats having hardly any birds recorded.

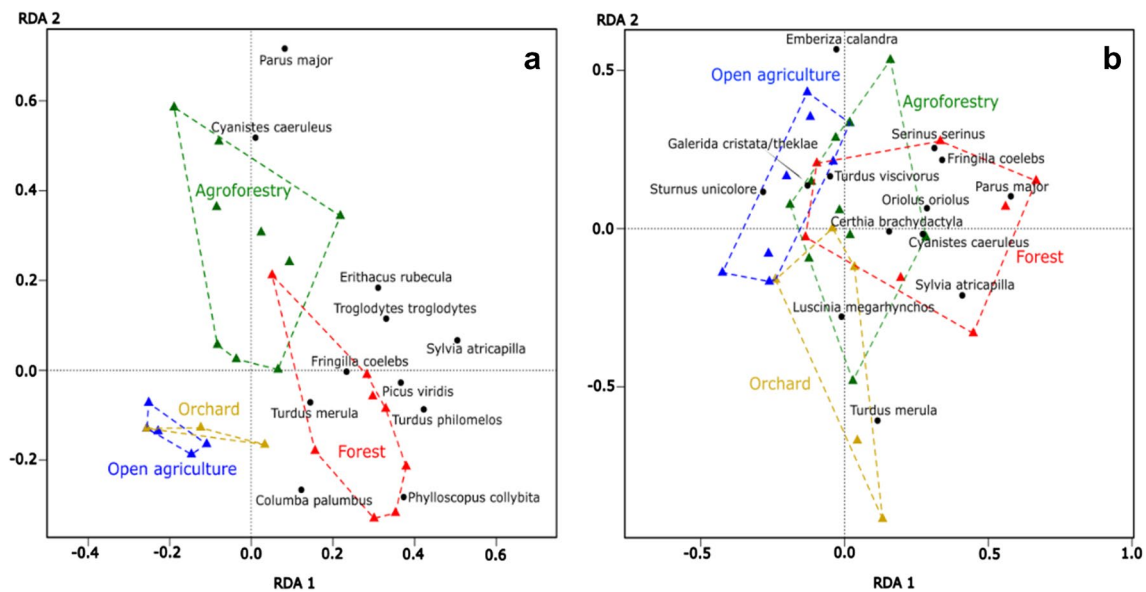


Fig. 4 Redundancy analysis (RDA) plots of the bird species communities in different habitats: agroforestry, forests, orchards, and open agriculture (cropland or pastures) in **a** temperate climate (England,

Germany, Switzerland, and Central France) and **b** Mediterranean climate (South of France, Italy, Spain, and Portugal). Dashed lines represent minimum convex polygons around habitat types.

In contrast, in the Mediterranean, the β diversity in agroforestry was not significantly different from the other habitats (Fig. 5a). Mediterranean open agriculture showed a higher distance to centroid compared to the temperate plots.

4 Discussion

This study clearly underpins the potential of mature agroforestry systems as a habitat of high value for birds in agricultural landscapes. As hypothesized, bird species richness

in agroforestry systems was higher than in open agriculture and similar to the species richness found in orchards and forests. In the Mediterranean, bird communities in agroforestry included both open and woody habitat species. However, in temperate Europe, no open habitat species were present in agroforestry plots which hosted only generalist and woody habitat bird species. As expected, in the temperate region, β diversity was significantly higher in agroforestry and forest than in open agriculture. Contrary to our expectations, β diversity within Mediterranean agroforestry did not differ significantly from other habitats.

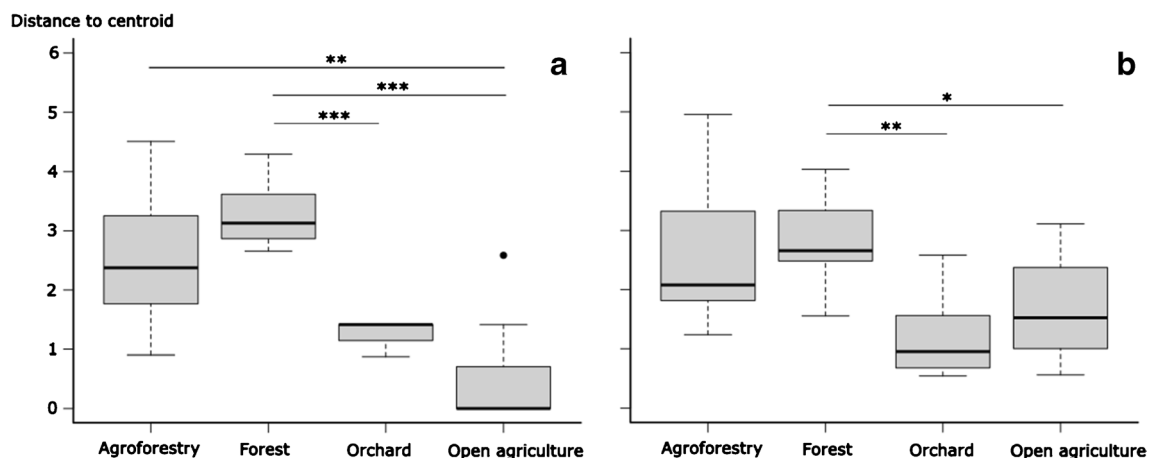


Fig. 5 β diversity within habitat types (agroforestry, forest, orchard, open agriculture (cropland/pasture)) in **a** temperate sites (England, Germany, Switzerland, and Central France) and **b** Mediterranean sites

(South of France, Italy, Spain, and Portugal). The y-axis shows the Euclidean distance to the centroid of the respective land-use type.

4.1 Species richness

Our results are in line with other studies which demonstrated that silvopastoral systems are hosting a greater bird diversity than open pastures (Hartel et al. 2014; McAdam et al. 2007; Morgan-Davies et al. 2008). The high bird diversity we found in both agroforestry and forest plots, and to a lesser extent in orchards, can be explained by the heterogeneity of these habitats. Structural diversity increases niche availability, providing more foraging, shelter, and nesting sites for birds over the season (Morelli 2013; Söderström et al. 2001). Old and dead trees with hollows and crevices, e.g., under the bark (Godinho and Rabaça 2011) represent habitats of high value for birds, especially for cavity-nesting species. Poulsen (2002) showed that the number of old trees, tree species, and tree size classes in Danish forests is correlated with a higher number of bird species and individuals. Moreover, a well-developed understory plays an important role for many shrub-dependent species (Fuller et al. 2007; Hartel et al. 2014). This diversity of niches is not only beneficial for birds, but for other taxa as well. McAdam et al. (2007) demonstrated that arthropods, an important food resource for birds (Holland et al. 2006), were more abundant in agroforestry and forest than in conventional agricultural fields. Pardon et al. (2019) and Boinot et al. (2019) highlighted the value of understory vegetation and grass strips for overwintering arthropods in temperate arable agroforestry. Söderström et al. (2001) showed that an increased heterogeneity and diversity in the shrub and tree layer within pastures lead to a higher species richness of insects and birds.

The lower diversity we found in orchards compared to forests is probably due to their higher disturbance and lower structural complexity, including a lower understory heterogeneity (Bohada-Murillo et al. 2019) compared to multi-layer and long-established forest ecosystems. As opposed to agricultural areas, woodlands show positive effects on the abundance of non-migratory birds in Germany (Schulze et al. 2019), which is confirmed by the high diversity we found in all forest plots.

Hence, higher ecosystem complexity and higher food availability in woody habitats, and particularly in forests and agroforestry sites, probably explain the higher bird species richness we found in those habitats in comparison with open agricultural land, in which the habitat spectrum for birds and other taxa is reduced. Our results are in line with other studies; however, due to differences in study design, site characteristics, and historical and geographical context, caution is needed with regard to comparability between results (Mupepele et al. 2021). The surrounding landscape is known to highly affect bird communities (Broughton et al. 2021; Söderström and Pärt 2000; Söderström et al. 2001). Söderström et al. (2001) found that pastures surrounded by arable land hosted a lower bird richness than pastures surrounded by forests. In the same way, isolated orchards showed a negative effect on birds whereas

habitat connectedness, i.e., proximity to forests, led to a higher bird species richness (Bailey et al. 2010). Moreover, land use history strongly affects biodiversity, which thus varies between older and newly established agroforestry systems (Mupepele et al. 2021). The value of tree-associated habitats increases with tree age (Poulsen 2002). We therefore expect the value of agroforestry systems for biodiversity to increase with time as well. The lack of biodiversity-related studies conducted in silvoarable systems, and especially alley-cropping systems, underlines that research in this area should be prioritized. Finally, several studies demonstrate the high value of birds as predators of invertebrates that support pest control services in agroecosystems (Barbaro et al. 2017; García et al. 2018). For example, great and blue tits, two species associated with agroforestry systems in our study, were identified as complementary predators of apple pest insects (García et al. 2021). In the present context of global change and the drastic decline in bird diversity and abundance, agroforestry sites could thus represent refuges for birds that support biological pest control in agricultural landscapes (Tscharntke et al. 2005).

4.2 Community composition and β diversity

Bird community composition differed between the four habitat types. In the Mediterranean sites, the results confirmed that bird communities in agroforestry comprised species of both open and woody habitats. However, in temperate sites, the bird communities of the agroforestry plots were mainly composed of generalist and woody habitat species while open agriculture and orchards were associated with a low diversity. In temperate Europe, β diversity was higher in agroforestry and forests compared to open agriculture. Similarly, in the Mediterranean, β diversity was higher in forests compared to open agriculture but no significant difference in β diversity between agroforestry and open agriculture was found. Temperate open agriculture showed a low β diversity compared to the same habitat in the Mediterranean. The differences observed between temperate and Mediterranean sites, especially concerning the open and semi-open habitats, can partly be explained by differences in agricultural intensity. The highly intensive farming in north-western Europe, associated with high crop yields and fertilizer applications, has led to a sharp decline in birds of open farmland habitats (Reif and Hanzelka 2020). This explains the low bird species richness as well as β diversity in temperate open agriculture. Almost no bird species of open and semi-open habitat were found in the temperate zone—neither in agroforestry nor in open agriculture. Birds of open and semi-open agricultural landscapes such as common whitethroat *Curruca communis*, circl bunting *Emberiza circlus*, or yellowhammer *Emberiza citrinella* have generally become rare in temperate Europe. In contrast, in the Mediterranean, due to more extensive land-use systems, open farmland habitats in many

areas still host a high biodiversity of birds and other taxa (Kleijn et al. 2009).

Given the higher species richness and β diversity of birds that we found in temperate agroforestry compared to open agriculture, this habitat is of high value for birds in temperate farmland. The presence of species relying on trees/shrubs for nesting and/or foraging in the agroforestry sites, such as green woodpecker *Picus viridis*, wren *Troglodytes troglodytes*, and great and blue tit *Parus major* and *Cyanistes caeruleus* confirm this. In temperate Europe, agroforestry systems may be particularly beneficial in the transition zone between forest and open farmland. In the intensively managed and highly fragmented European farmland, agroforestry could act as stepping stones (habitat islands) or ecological corridors and could thus contribute to the facilitation of animal movement and plant dispersion (Fischer et al. 2006; Hidalgo et al. 2021; Jongman et al. 2004).

In accordance with other studies (Tellería 2001), our results show that Mediterranean agroforestry hosts both woodland and open habitat bird species. Open habitat species, such as larks *Galerida sp.* and corn bunting *Emberiza calandra*, relying on low vegetation for nesting and foraging, were present in agroforestry as well as in open agriculture. Moreover, generalist/semi-open habitat species like European serin *Serinus serinus* and great tit *Parus major* were also found in agroforestry sites, as well as in forests. Finally, the presence of species such as short-toed treecreeper *Certhia brachydactyla*, blue tit *Cyanistes caeruleus*, or golden oriole *Oriolus oriolus* in both forest and agroforestry confirms the value of agroforestry for woody habitat species that rely on dense woody vegetation for nesting and/or foraging (Godinho and Rabaça 2011). Those results are in line with studies showing that the Spanish dehesas, whose semi-open physiognomy and habitat diversity are the result of centuries of extensive grazing management, act as an ecotone habitat, hosting a high bird diversity composed of species relying on open and border habitat as well as forest species (Tellería 2001).

In the Mediterranean, the lower differences in species composition and β diversity that we measured between habitats (distance to centroid) could be due to a higher habitat and landscape heterogeneity compared to the temperate sites. For example, in the open pasture plots in Spain, scattered trees or shrubs provided valuable structures for birds. In the same way, woody control plots often showed gaps with low vegetation or with a lower tree density. Therefore, numerous tree/shrub-dependent species, e.g., nightingale *Luscinia megarhynchos* or chaffinch *Fringilla coelebs*, occurred in Mediterranean forests and agroforestry as well as open agriculture.

Our findings suggest that agroforestry, through increasing heterogeneity at field and landscape scale, favors mostly generalist bird species as also supported by other authors (Batáry et al. 2011; Filippi-Codaccioni et al. 2010; Söderström et al.

2001; Pickett and Siriwardena 2011). In contrast, as shown by numerous studies (Báldi and Batáry 2011; Batáry et al. 2011; Hagist and Schürmann 2021; Reif and Hanzelka 2020), some specialist species, such as birds of semi-natural grassland or arable land such as the skylark *Alauda arvensis*, are not favored or can even be deterred by the establishment of woody structures. Hence, the implementation of new agroforestry systems needs to be adapted to regional conditions and the geographical as well as historical context (Reisner et al. 2007).

Our results show that agroforestry can support a high diversity of breeding birds in both temperate and Mediterranean Europe; however, the added value of those systems differs between the regions. As demonstrated within this study, agroforestry can act as an important refuge for generalist and forest species in intensively managed, tree-poor agricultural areas in temperate Europe. However, they do not necessarily bring back the farmland birds that have declined so drastically over the past decades (Voříšek et al. 2010). In southern Europe where open semi-natural habitats and low-intensity agricultural systems with high bird species richness are still relatively common but threatened by both agricultural intensification and abandonment, agroforestry systems can represent an important intermediate habitat for both open/semi-open habitat and forest bird species.

5 Conclusion

To our knowledge, this is the first study examining the bird diversity in mature European agroforestry systems across multiple countries. Confirming our hypothesis, we found that agroforestry systems supported bird diversity as they hosted a higher species richness than open agricultural systems in temperate as well as in Mediterranean countries. However, the effect of agroforestry systems on bird diversity was different in temperate compared to Mediterranean sites and hence highly dependent on the regional context. Through providing heterogeneity in agricultural landscapes, agroforestry systems may help to restore farmland bird diversity in temperate regions of Europe and to halt biodiversity loss in the Mediterranean. In general, agroforestry systems are a promising example of agricultural production that is compatible with biodiversity conservation. Positive effects of agroforestry on ecosystem functions and resilience could contribute to ecological intensification, e.g., via improved pest regulation also in surrounding crops.

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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.

Code availability Not applicable

Declarations

Ethics approval Not applicable

Consent to participate and for publication Not applicable

Conflict of interest The authors declare no competing interests.

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CHAPTER III

AGROFORESTRY SYSTEMS FAVOR BAT CONSERVATION BUT ONLY WHEN OLD AND GRAZED

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Original research article

Agroforestry systems favor bat conservation but only when old and grazed

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ABSTRACT

As a consequence of agricultural intensification and landscape homogenization, semi-natural elements such as hedges, woodland patches and scattered trees have been removed from many agricultural areas. The resulting habitat loss has led to the decline in the diversity and abundance of many taxa including bats, which are highly dependent on woody plants for foraging, roosting and reproduction. By combining trees with crops (silvoarable systems) or livestock (silvopastoral systems), agroforestry re-integrates structural diversity into agricultural areas that could have beneficial effects on biodiversity. In this study, bat activity was recorded with autonomous sound recorders (AudioMoth) in sixty-five agroforestry and reference sites across western Europe. Bat activity in silvopastoral systems was two times higher than in pastures and orchards and four times higher than in cropland. In addition, social calls and foraging rates of bats were highest in silvopastoral systems. By contrast, bat activity was not higher in silvoarable systems compared to control plots. Tree characteristics affected total bat activity, which was higher with increased tree age and in sites with broad-leaved compared with coniferous trees. Our results show that the combination of old broad-leaved trees and livestock is highly beneficial for bats. Thus, silvo-pastoral systems deserve more attention in sustainable agriculture and biodiversity conservation.

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However, management should also be considered and especially the implementation of silvo-pastoral systems with low-intensity grazing and low pesticide input should be supported.

1. Introduction

Agricultural intensification has considerably modified European landscapes. Semi-natural habitats such as hedges and woodland patches as well as scattered trees have been removed, leading to a decrease in landscape diversity (Stoate et al., 2001; Robinson and Sutherland, 2002). The resulting loss of shelters, roosting sites, foraging habitats and food resources has led to severe population declines in farmland biodiversity (e.g. Fahrig, 2003) including insects (e.g. Raven and Wagner, 2021), birds (Donald et al., 2001; Benton et al., 2002) and mammals (Pekin and Pijanowski, 2012). Likewise, bat populations have been affected by land use changes and suffered drastic declines during the 20th century, in part due to reduced roost and prey availability (Mickleburgh et al., 2002; Park, 2015; Treitler et al., 2016). Across Europe, bat conservation is supported by several conventions (e.g. Bern and Bonn conventions (Council of Europe, 1979, United Nations Environment Programme, 1979)), agreements (e.g. EUROBATS Agreement (United Nations Environment Programme/Eurobats/Eurobats/Eurobats, 1991)) and actions plans (e.g. Action Plan for the Conservation of Bat Species in the European Union (European Commission/Eurobats, 2018)) and bats are legally protected in the European Union (Article 12 of the Habitat Directive, 92/43/CEE (European Union, 1992)). However, bat populations remain under pressure from anthropogenic threats, especially in agricultural areas where they face habitat change and roost disturbance (European Commission/Eurobats, 2018; Frick et al., 2019). Their low reproduction rate, long lives and high metabolic requirements make bats sensitive to human activities and environmental change (Jones et al., 2009).

Bat sensitivity, combined with their presence in a wide range of ecosystems, make these mammals important bioindicators of wider biodiversity values (Jones et al., 2009). As insectivorous bats need a large quantity of insect prey to fulfil their energy requirements (Arthur and Lemaire, 2015; Russo et al., 2021), their foraging activity closely correlates with insect availability. The activity of European bats was shown to increase in the presence of cattle and dung, which attract numerous insects (Downs and Sanderson, 2010; Ancillotto et al., 2017). Moreover, previous studies have shown a positive effect of nearby forests, tree lines or isolated trees, hedgerows, tree groves (Boughey et al., 2011; Heim et al., 2015; Finch et al., 2020) on bat activity as well as on species richness. Especially old and broad-leaved trees are known to represent foraging and roosting habitats of higher value for bats compared to younger and coniferous tree stands, often associated to shorter rotation periods (Boye and Dietz, 2005; Russo et al., 2016; Charbonnier, 2016a and 2016b). Dense networks of linear woody features within a landscape represent important landmarks for bats and are used both as commuting routes (e.g. between roosts and foraging areas) and for foraging (Verboom and Huitema, 1997; Heim et al., 2015).

By deliberately combining trees with crops (silvoarable systems) or livestock (silvopastoral systems) on the same land, agroforestry adds structural diversity to farmland (Nair, 1993). The biophysical interactions between the woody and non-woody components support ecosystem services (Jose, 2009; Mosquera-Losada et al., 2009; Palma et al., 2007) such as water retention (Joffre and Rambal, 1988) or nutrient cycling (Nair, 2007; Torralba et al., 2016) and can result in both economic and ecological advantages. The high heterogeneity due to the presence of trees and/or shrubs in agroforestry also benefits biodiversity by providing shelter, food, roosting and breeding opportunities for many organisms (Jose, 2009; McAdam and McEvoy, 2009; Torralba et al., 2016; Mupepele et al., 2021). Agroforestry has been shown to benefit arthropods (Boinot et al., 2019; Pardon et al., 2019), birds (Edo et al., 2024) and mammals (Klaa et al., 2005; Gonçalves et al., 2012) all of which can promote ecosystem services such as pest control (Boinot et al., 2019; Staton et al., 2019). Although it has been demonstrated that agroforestry supports biodiversity and that bat activity is higher if linear elements and grazing animals are present in the landscape (Ancillotto et al., 2017), to our knowledge, no previous studies have specifically focused on bats in agroforestry systems at a European scale. Therefore, this study aims to elucidate the effects of agroforestry on bat richness and activity to inform and adapt conservation strategies for these European-wide protected mammals and in turn derive potential benefits to agriculture, since bats play a major role in the control of pest insects (Boyles et al., 2011; Kunz et al., 2011; Ancillotto et al., 2017).

We predict that bat activity is higher in agroforestry systems, due to higher structural heterogeneity, compared with open agriculture (cropland and pastures) as well as compared with orchards. Given that grazing livestock attract numerous insects and that low-intensity grazing also contributes to habitat heterogeneity, we predict that grazing has a positive effect on bat activity. Overall, we predict bat activity to increase in grazed habitats (pastures and silvopastures) and in plots associated with woody elements (forests, agroforestry), as bats often depend on vegetation structures for both commuting and foraging. Hence, we predict more positive effects of silvopastoral than of silvoarable systems on bat activity. We predict that coniferous and broad-leaved trees will differently affect bat activity and we expect an increase of bat activity with tree age as both increasing age and broad-leaved trees are known to represent roosting and foraging habitats of high value for bats.

2. Material and methods

2.1. Study sites

The study was carried out in eight different geographical regions. In each region we selected an agroforestry farm (in the following referred as “site”) including either silvoarable agroforestry (combination of trees and crops) or silvopastoral agroforestry systems (combination of trees and livestock) and nearby control plots. The sites were located in seven countries across Europe: England,

Switzerland, France (two sites) Germany, Italy, Portugal, and Spain (Fig. 1). We assessed bat diversity and activity in one to three agroforestry fields per site (hereafter termed as “plots”). In total we sampled seven silvoarable plots located in Southern France, Switzerland and England and thirteen silvopastoral plots located in Spain, Portugal, Italy, Central France and Germany. For each agroforestry plot, two to three control plots with the same woody or agricultural components were sampled. Thus, in addition to the silvoarable systems, a total of seven croplands (with the same crop as in the agroforestry system), ten forests and four orchards (with the same tree species as in the agroforestry system) were sampled. Similarly, 13 open pastures, 16 forests and five orchards were sampled as control plots for the silvopastoral systems. We defined the forests as areas with more than 10 percent tree cover over at least 0.5 ha and with part of the trees aged more than 30 years, but excluding trees of agricultural production systems (FAO Food and Agriculture Organization of the United Nations, 2018). Fruit or nut orchards ($n = 9$) were sampled if the trees in the agroforestry system were fruit or nut trees (i.e. in Germany, Switzerland, in Southern France and in Portugal). Agroforestry and control plots of a same site were located nearby, to minimize the variation of e.g. climate, soil, and the surrounding landscape (coordinates of each plot are given in Supporting Table A1). The minimum distance between plots of the same site was 200 m, to avoid any overlap of the bat call recordings. We selected mature agroforestry and orchard plots with trees planted at least 12 years ago. Hereafter, the time since planting will be referred to as “tree age”, irrespective of age of the trees at the time of planting which is not always known. The trees of the silvoarable plots in Switzerland (*Malus domestica*, *Prunus avium*), England (mixed broad-leaved tree stands) and Southern France (*Juglans regia*, *Pinus* spp.) were at least 12, 25 and 27 years old, respectively. The trees of the silvopastoral plots were 20 (Germany, *Malus domestica*), 25 (Portugal, *Pinus* spp.), 35 (Central France, *Acer pseudoplatanus*, *Fraxinus excelsior* and *Prunus avium*), 90 (Italy, *Quercus* spp.) and 175 (Spain, *Quercus* spp.) years old. The control orchards and forests were stocked with trees of the same species and of approximatively the same age as those in the respective agroforestry site. Information on management, environmental parameters, tree species and crops associated to each plot as well as sampling dates can be found in Supporting Table A1.

2.2. Data collection

We assessed bat activity via analysis of the echolocation calls they use to detect prey and for orientation, and analysis of social calls. Autonomous sound recorders (AudioMoth V1.1.0, Open Acoustic Devices, firmware version 1.7., configuration app version 1.6.0; Hill et al., 2019) were mounted on a thin pole at a height of 1.5 m, with the microphone oriented towards the respective plot's centre. In each plot one AudioMoth was set up three times between March and July in 2021 (England, Germany, Switzerland and Central France) and 2022 (Southern France, Italy, Portugal and Spain). See Supporting Table A1 for the detailed sampling dates. Recorders were placed at least 20 m from the plot's edge to record only individuals active within the studied habitat (Fuentes-Montemayor et al., 2013) and rotated between plots for each sampling to reduce possible hardware bias. AudioMoths were wrapped in a single layer of clingfilm to protect them from humidity and dust. We conducted surveys during calm and dry weather (i.e., wind force between 0 and 1 on the Beaufort scale and no precipitation), as bat activity is strongly reduced during wind or rain (Arthur and Lemaire, 2015). During each of the three samplings, the AudioMoths were set to record continuously from ninety minutes before sunset until ninety minutes after sunrise. Full night recordings with continuous sampling allow the detection of more species and can account for varying activity of bats during the night (Skalak et al., 2012). Devices were programmed to record at medium gain, a recording duration of 3595 s and sleep

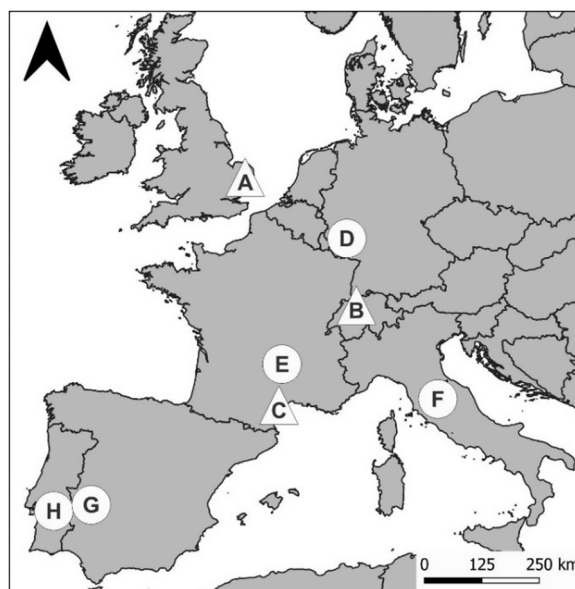


Fig. 1. Geographic location of the silvoarable (A-C) and silvopastoral (D-H) study sites.

Triangles = silvoarable systems, circles = silvopastoral systems, A = Wakelyns (UK), B = Eulenhof and Sursee (CH), C = Restinclières (FR), D = Bannmühle (DE), E = Lamartine (FR), F = Tenuta di Paganico (IT), G = Dehesa de Majadas (ES), H = Moinhos de Vento (PO).

duration of 5 s. The sampling rate of 192 kHz was suited to record all bat species of the study region except for *Rhinolophus euryale* and *R. hipposideros*. Recordings were saved as .wav files and stored on memory cards (SanDisk Corporation, Milpitas, California, USA). The same recordings, but different time windows were used to study birds in a previous study (Edo et al., 2024), which is the reason why the sampling took place in spring.

2.3. Species identification

The audio recordings from each site were split into one-minute files and pre-classified using the software Kaleidoscope Pro (version 5.4.8; Auto-ID: Bats of Europe classifier version 5.4.0 with European region database corresponding to each country; Wildlife Acoustics Inc., Concord, MA, USA). The software Kaleidoscope detects bat signals with a frequency range between 8 and 120 kHz, a pulse length in the range of 2 and 500 ms and a maximum of 500 ms inter-syllable gap. Files without any detected bat signals following these criteria were filtered out as “noise files” by the software and were not further analyzed. Files containing three (or fewer) bat calls recognized by the software as well as files misidentified by the software (e.g. vocalization of birds, orthoptera, anthropogenic noise) were manually assigned to “noise files”. Spectrogram parameters used were an FFT (Fast Fourier Transform) size of 512 and a Win size of 128 in an overlapping Hann window.

All one-minute files associated with a bat species or associated with the label “No-ID” were manually verified to avoid errors due to automatic identification (Russo and Voigt, 2016; Rydell et al., 2017). Each bat pass (defined as three or more echolocation calls recognized by Kaleidoscope within one second of each other) was identified at species level for *Barbastella barbastellus*, *Hypsugo savii*, *Pipistrellus pipistrellus*, *Rhinolophus ferrumequinum* and *Tadarida teniotis*. Due to the similarities in call structures and frequencies and difficulties to distinguish between species especially in cluttered environments, we assigned several bat species to species groups/sonotypes: *Pipistrellus nathusii*/P. kuhlii, *Pipistrellus pygmaeus*/Miniopterus schreibersii, *Myotis* spp., *Plecotus* spp. and Nyctaloid sonotype (Schnitzler and Kalko, 2001; Heim et al., 2015; Russo and Voigt, 2016; Rydell et al., 2017). The Nyctaloid sonotype potentially included the species *Eptesicus isabellinus*, *E. nilssonii*, *E. serotinus*, *Nyctalus lasiopterus*, *N. leisleri*, *N. noctula* and *Vespertilio murinus*. *Myotis* spp. and *Plecotus* spp. potentially included all *Myotis* and *Plecotus* species from the study area. We identified the different bat species on the basis of their calls' shape, regularity, recurrence, and signal structure as well as signal measurements such as maximum energy frequency, bandwidth, call duration, start and end frequency, maximum and minimum frequency, characteristic frequency, and inter-pulse interval (Barataud, 2020; Russ, 2021; Skiba, 2009; Jamault et al., 2018).

In addition to the total activity (total number of active minutes for each species), we counted feeding buzzes in the final approach towards prey before capture, as well as social calls, used for intra- and inter-species communication (Russ, 2021). A maximum of one individual per bat species, one feeding buzz and one social call was counted per one-minute file. We quantified bat activity during the sampling period by summing the total number of minutes containing bat passes (“active minutes”, further referred as “activity”) for each species/species group (Froidevaux et al., 2017; Kalcounis et al., 1999). In addition to the general activity, foraging activity was quantified by calculating the feeding buzz rate as the number of minutes with feeding buzzes per number of active minutes following Eq. (1):

$$\text{Feeding buzz rate}_i = \frac{n_{\text{feeding buzzes}_i}}{n_{\text{active minutes}_i} + 1} \quad (1)$$

Similarly, the social call rate was quantified as the number of minutes with social calls per number of active minutes following Eq. (2):

$$\text{Social call rate}_i = \frac{n_{\text{social calls}_i}}{n_{\text{active minutes}_i} + 1} \quad (2)$$

with $n_{\text{feeding buzzes}_i}$ (1) the number of minutes with feeding buzzes, $n_{\text{social calls}_i}$ (2) the number of minutes with social calls in each plot i, and $n_{\text{active minutes}_i}$ the total number of active minutes recorded in each plot across the three sampling dates.

2.4. Statistical analysis

In a first step, in order to analyze the effect of habitat type on bat activity, we fitted linear mixed-effect models with habitat type as explanatory variable (equation: lmer (Activity ~ Habitat + (1|Site)), R package lme4, Bates et al., 2015). Due to the nested design of the study, “Site” was used as a random factor. Post hoc tests were used to determine the pairwise differences of the total activity, social call rate and feeding buzz rate between habitats (R package emmeans, function emmeans, Lenth, 2022). In a second step, we fitted linear mixed-effect models to analyze the effect of tree type (broadleaved or conifer) and tree age on bat activity, again with “Site” as a random factor (equation: lmer (Activity ~ log10(Age) + Tree type + (1|Site)). All models were tested against their respective null model to ensure that ΔAIC was > 2 .

For all statistical tests, P-values < 0.05 were considered as significant. P-values, means and standard errors of the mean (SE) are given in text and tables. All statistical analyses were conducted in R version 4.2.2 (R Core Team, 2022).

3. Results

In total, 10 species and species groups (hereafter call types) were recorded (Table 1). The most common call types were *Pipistrellus*

pipistrellus (present on 83 % of all plots), *Pipistrellus nathusii*/*P. kuhlii* (78 %) and *Myotis* (77 %). Almost all call types were recorded in all habitats (Table 1).

Over all sites and across all species, 7890 active minutes were recorded, including 629 minutes with feeding buzzes and 749 minutes with social calls. Together, the *Pipistrellus* species represented 78 % of the total activity recorded (Table 1). Bat activity was highest in silvopastoral plots and differed significantly from forests, cropland, pastures and marginally significantly from silvoarable and orchard plots (Fig. 2, Table 1 and Supporting Table A2). Bat total activity was four times higher in silvopastoral plots relative to cropland, more than two times higher than in silvoarable plots, orchards and pastures and 1.5-times higher than in forests. *Pipistrellus nathusii*/*P. kuhlii* was the dominant sonotype in silvopastures, accounting for nearly half of total bat activity. Their activity was more than three times higher in silvopastures than in pastures and silvoarable systems, more than two times higher than in forests and more than six times higher than in orchards and cropland (Table 1). Similarly, *Rhinolophus ferrumequinum*, *Pipistrellus pipistrellus* and the species groups *Myotis*, *Pipistrellus pygmaeus*/*Miniopterus schreibersii* had their highest activity in silvopastoral systems compared to the other habitats, though differences were not significant. Nyctaloid activity was more balanced between habitat types. As an exception, *Tadarida teniotis* showed a higher activity in pastures compared to the other habitats (Table 1).

The feeding buzz rate was higher in silvopastures compared to pastures, but the difference was not significant (Fig. 3a, Table 1, Supporting Table A3). The social call rate was significantly higher in silvopastoral systems and forests relative to pastures (Fig. 3b, Table 1 and Supporting Table A3).

Bat activity depended on tree type and was on average ten times higher in plots with broad-leaved trees (Spain, France-Lamartine, Italy, Germany, France-Restinclières, Switzerland and England) compared with coniferous trees (Portugal, France-Restinclières) (Fig. 4). In addition, bat activity increased with tree age. The steepest increase in activity was found up to a tree age of around 50 years. A further increase in tree age led to a gradual saturation in activity (Fig. 5).

Table 1

Bat activity $\pm$ standard error of bat species/species groups recorded in silvoarable and silvopastoral plots, forests, orchards, cropland and pastures; letters show significant pairwise differences between habitats derived from post hoc test.

Species/Habitat	Silvoarable (n = 7)	Silvopastoral (n = 13)	Forest (n = 16)	Orchard (n = 9)	Cropland (n = 7)	Pasture (n = 13)	Total activity per species	Mean activity per species
<i>Barbastella barbastellus</i>	0 $\pm$ 0	0.23 $\pm$ 0.17	0.06 $\pm$ 0.06	0 $\pm$ 0	0 $\pm$ 0	0.23 $\pm$ 0.17	7	0.11 $\pm$ 0.05
<i>Hypsugo savii</i>	0.29 $\pm$ 0.29	0.92 $\pm$ 0.37	1.06 $\pm$ 0.60	0.89 $\pm$ 0.77	1 $\pm$ 0.43	1.92 $\pm$ 1.36	71	1.09 $\pm$ 0.33
<i>Pipistrellus pygmaeus</i> / <i>Miniopterus schreibersii</i>	11.71 $\pm$ 10.73	42.77 $\pm$ 26.39	25.5 $\pm$ 8.64	8 $\pm$ 7.26	7.29 $\pm$ 5.98	5.69 $\pm$ 2.58	1243	19.12 $\pm$ 6.01
<i>Myotis</i> spp.	3 $\pm$ 1.51	14.62 $\pm$ 4.91	8.56 $\pm$ 3.65	2.11 $\pm$ 1.39	4.43 $\pm$ 2.66	5.62 $\pm$ 1.37	471	7.25 $\pm$ 1.47
Nyctaloid	4.86 $\pm$ 2.53	27.69 $\pm$ 17.06	8.75 $\pm$ 3.34	27.33 $\pm$ 11.21	5.57 $\pm$ 2.51	20.77 $\pm$ 7.30	1089	16.25 $\pm$ 4.15
<i>Pipistrellus nathusii</i> / <i>P.</i> <i>kuhlii</i>	14.57 $\pm$ 7.77 ab	84.69 $\pm$ 28.11 a	35.56 $\pm$ 13.31 b	6.44 $\pm$ 3.04 ab	13.29 $\pm$ 7.59 ab	28.08 $\pm$ 10.86 b	2288	35.20 $\pm$ 7.53
<i>Pipistrellus pipistrellus</i>	29.29 $\pm$ 7.69	44.54 $\pm$ 17.22	51.88 $\pm$ 13.77	33.56 $\pm$ 14.17	20.29 $\pm$ 3.92	15.31 $\pm$ 5.63	2257	34.72 $\pm$ 5.53
<i>Plecotus</i> spp.	1.14 $\pm$ 0.63	1.46 $\pm$ 0.91	1.44 $\pm$ 0.48	0.22 $\pm$ 0.15	1.71 $\pm$ 0.89	2.92 $\pm$ 1.55	102	1.57 $\pm$ 0.40
<i>Rhinolophus ferrumequinum</i>	0 $\pm$ 0	0.77 $\pm$ 0.54	0.5 $\pm$ 0.18	0 $\pm$ 0	0.14 $\pm$ 0.14	0.15 $\pm$ 0.11	21	0.32 $\pm$ 0.12
<i>Tadarida teniotis</i>	0.43 $\pm$ 0.43 ab	2.54 $\pm$ 1.40 ab	1.31 $\pm$ 0.49 b	0.78 $\pm$ 0.55 ab	0.86 $\pm$ 0.70 ab	20.85 $\pm$ 12.19 a	341	5.25 $\pm$ 20.75
Total activity ^a	65.29 $\pm$ 27.49 b	220.23 $\pm$ 52.23 a	134.62 $\pm$ 22.45 b	79.33 $\pm$ 24.79 ab	54.57 $\pm$ 18.89 b	101.54 $\pm$ 23.3 b	-	-
Feeding buzzes	6.29 $\pm$ 2.29 ab	23.46 $\pm$ 6.86 a	11.5 $\pm$ 3.24 ab	4 $\pm$ 1.57 b	4 $\pm$ 1.93 b	2.46 $\pm$ 0.83 b	629	9.68 $\pm$ 1.86
Feeding buzzes rate	0.08 $\pm$ 0.03 ab	0.15 $\pm$ 0.07 a	0.07 $\pm$ 0.01 ab	0.03 $\pm$ 0.01 ab	0.06 $\pm$ 0.03 ab	0.02 $\pm$ 0.01 b	-	0.07 $\pm$ 0.02
Social calls	2 $\pm$ 1.31 ab	32.23 $\pm$ 12.35 a	16.19 $\pm$ 5.22 ab	3.33 $\pm$ 2.49 ab	1.71 $\pm$ 1.25 ab	0.92 $\pm$ 0.38 b	746	11.48 $\pm$ 3.11
Social calls rate	0.01 $\pm$ 0.01 ab	0.11 $\pm$ 0.03 a	0.11 $\pm$ 0.03 a	0.02 $\pm$ 0.01ab	0.03 $\pm$ 0.02ab	0.01 $\pm$ 0.00 b	-	0.06 $\pm$ 0.01

^a number of active minutes; feeding buzzes and social calls excluded

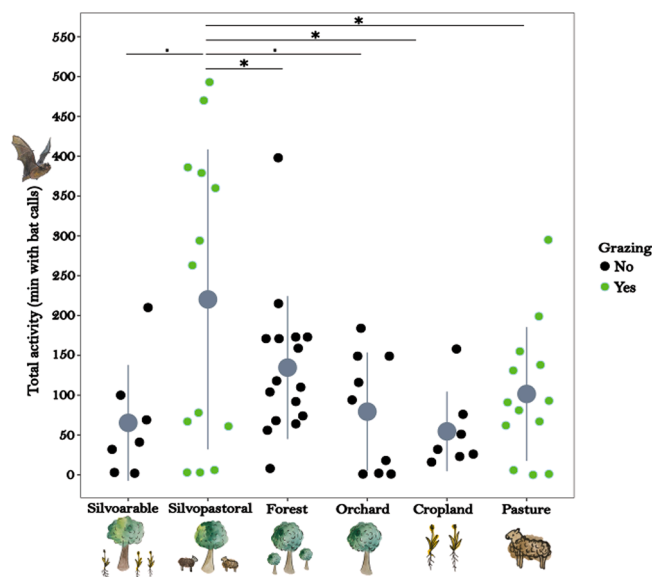


Fig. 2. Bat total activity (number of active minutes) in agroforestry (silvoarable $n = 7$, silvopastoral $n = 13$), forest ($n = 16$), orchards ($n = 9$) and open agriculture (cropland $n = 7$, pasture $n = 13$). Significance levels: . $P < 0.1$, * $P < 0.05$. Grey dots indicate mean values. See [Table 1](#) for the detailed results of activity ($\pm$ SE) in each habitat. See [Supporting Table A3](#) for the results of the mixed-effect models and post hoc tests used to determine the pairwise differences between habitats.

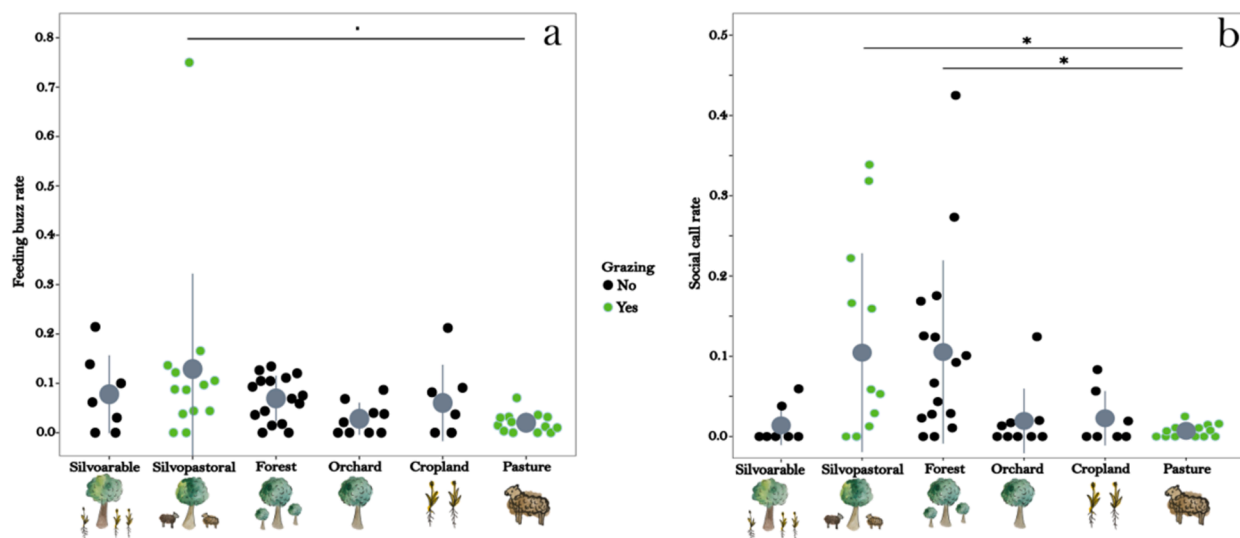


Fig. 3. Feeding buzz rate (a) and social call rate (b) in agroforestry (silvoarable $n = 7$, silvopastoral $n = 13$), forest ($n = 16$), orchards ($n = 9$) and open agriculture (cropland $n = 7$, pasture $n = 13$). Significance levels: . $P < 0.1$, * $P < 0.05$. Grey dots indicate mean values. See [Table 1](#) for the detailed results of activity ($\pm$ SE) in each habitat. See [Supporting Table A4](#) for the results of the mixed-effect models and post hoc tests used to determine the pairwise differences between habitats.

4. Discussion

In line with our hypotheses, our results clearly underline the high value of silvopastoral agroforestry systems for bats. The presence of woody elements combined with livestock had a positive effect on bat activity. Bat activity was higher in silvopastoral systems than in all other habitats, both habitats with trees (silvoarable systems, forests, orchards) and without (cropland and pastures). In addition, feeding and social activity were higher in silvopastures compared with pastures. Broad-leaved trees were associated with a higher bat activity compared with coniferous trees and activity increased with increasing tree age. This suggests that across the studied European agroclimatic zones, silvopastoral systems with mature broad-leaved trees are of outstanding value for the foraging and socializing of bats. However, in our study, coniferous tree stands tended to be younger than broadleaved trees, as well as silvoarable systems being

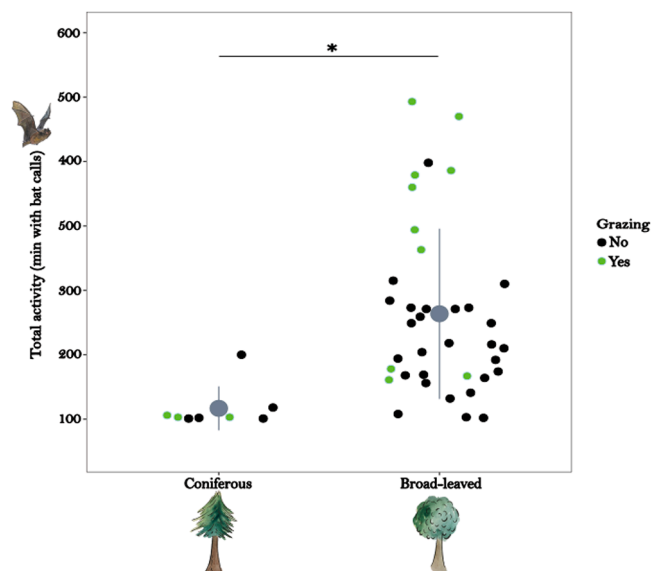


Fig. 4. Comparison of bat total activity (number of active minutes) between plots with coniferous trees (silvoarable $n = 1$, silvopastoral $n = 3$, orchards $n = 4$) and plots with broad-leaved trees (silvoarable $n = 6$, silvopastoral $n = 10$, forest $n = 16$, orchards $n = 6$). Significance levels: $*P < 0.05$. Grey dots indicate mean values.

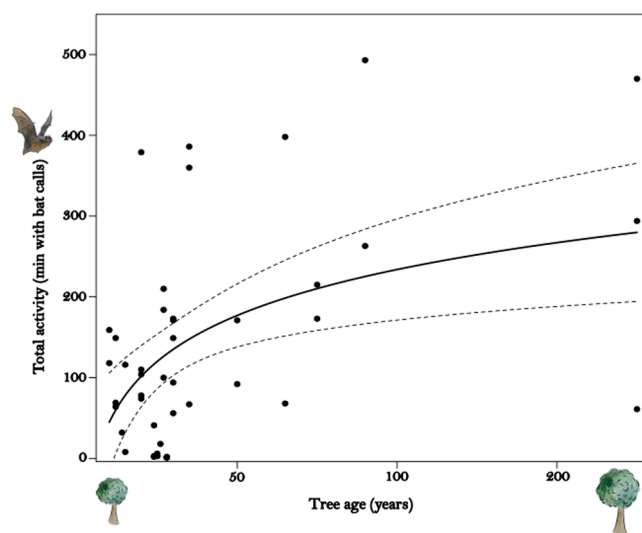


Fig. 5. Effect of tree age on bat total activity (number of active minutes) in agroforestry plots (silvoarable $n = 7$, silvopastoral $n = 13$), forests $n = 16$ and orchards $n = 9$. Predicted response (black line) and associated 95 % confidence intervals (dashed lines).

younger when compared to silvopastoral systems (Supporting Table A1). Consequently, the separation of the effects of tree type and tree age would require additional study of a larger set of agroforestry systems with more balanced age between conifers and broad-leaved trees, both in silvoarable and silvopastoral systems. The observed differences between habitat types are probably caused by differences in habitat structure and prey availability, which are in turn driven by the presence, age and type of trees, and by the cropping or grazing regime.

4.1. Effects of trees

The presence of trees has a strong influence on bats because woody structures represent important shelter and foraging habitats for them. Bat activity has thus been shown to increase near single trees (Fischer et al., 2010), tree lines and hedges (Boughey et al., 2011; Froidevaux et al., 2019; Wickramasinghe et al., 2003). Linear woody landscape features serve as flight paths for bats, for example between their roosts and feeding habitats (Heim et al., 2015; Verboom and Huitema, 1997). Finch et al. (2020) and Treitler et al.

(2016) showed that bat activity was higher near linear woody features than in the middle of agricultural fields. In addition to increasing foraging efficiency by concentrating insect prey, linear vegetation elements facilitate the navigation of echolocating bats and offer them protection from wind and from predators relying on vision (Verboom and Spoelstra, 1999; Downs and Racey, 2006; Froidevaux et al., 2019). Considering this, bats in silvopastoral systems may leave their roosts earlier than in treeless areas, which would enable them to forage for a longer time and consume more prey (Russo et al., 2007). The higher rates of feeding buzzes in silvopastoral systems relative to pastures further underlines the high value of silvopastoral systems as foraging habitat. During our recording season, bats use social calls to communicate with other individuals, for example as territorial or hunting area occupancy calls (Arthur and Lemaire, 2015) or to indicate the location of the roost. Hence, the high rates of social calls in silvopastoral systems and forest underline their importance as foraging habitat. The high social call rates in silvopasture and forest may indicate additional functions for roosting, especially when compared to e.g. open pastures that had high bat activity but distinctly fewer social calls.

Our results show that, irrespective of habitat type, bat activity is highly influenced by tree age and tree species composition (Downs and Racey, 2006; Russo et al., 2016), which are both known to correlate with roosting opportunities. The steep increase in bat activity we measured up to a tree age of around 50 years suggests that the woody habitats with the highest ecological value for bats are those with mature trees. As trees age they develop more cavities and other roosting sites, not only for bats but also for their prey (Boye and Dietz, 2005; Russo et al., 2016). Traditional silvopastoral agroforestry systems have long been known to support high biodiversity (e.g. Herzog, 1998; Moreno et al., 2016; Torralba et al., 2016) and Russo et al. (2005) already showed their importance for the bat species *Rhinolophus mehelyi* in the Dehesas region of Spain. Furthermore, older trees with their larger crowns may also provide more effective shelter from wind and predators (Downs and Racey, 2006). The higher bat activity measured in plots with broad-leaved trees compared with coniferous trees is in line with previous studies (Entwistle et al., 1996; Walsh and Harris, 1996; Boye and Dietz, 2005; 2006) but in contrast with the study of Węgiel et al. (2023) who found no differences in bat activity between coniferous, deciduous and mixed tree stands. The often reduced attractiveness of coniferous tree stands for bats may be explained by a lower insect prey availability (Lepidoptera: Entwistle et al., 1996) as well as a lower availability of suitable roosting cavities for bats relative to broadleaved tree stands (Boye and Dietz, 2005; Russo et al., 2016). The differences in bat activity we measured between coniferous and deciduous tree plantations could also have been influenced, beyond the tree species, by other characteristics as spatial structure, clutter condition, management or habitat fertility (Węgiel et al., 2023). In our study, coniferous tree stands had slow growing trees (particularly in Portugal) due to the arid climate prevailing in the Mediterranean, which probably contributed to a low habitat quality of those trees for bats.

An important limitation with respect to our habitat comparison is that bat calls are transmitted further in open habitats than in densely cluttered environments (Haupt et al., 2023; Sugai et al., 2020). This can lead to a declining sampling efficiency of acoustic recorders from open habitats over orchards/agroforestry to forest. This could affect our results with respect to bat activity. The reduced transmission in cluttered environments means that the true positive effects of agroforestry over open agriculture areas are likely higher than recorded in the current study, since sampling efficiency was likely reduced in agroforestry relative to open land. By contrast, the 1.5 times higher bat activity in silvopastures compared to forest may be an artefact of higher sampling efficiency in the more open silvopastures. Such limitations in the comparison of different habitat types can be overcome through the measurement of sound detection spaces (Darras et al., 2016), which would however be a major effort that was not feasible in the multiple sampling sites of the current study.

Another possible bias from our study design is the spatial proximity of forest, agroforestry and open agricultural plots. This likely means that open agricultural reference plots are closer to woody habitats than average open agricultural fields, and thus not fully representative. Since bat activity tends to decrease with distance from forest (e.g., Chavez et al. in press; Heim et al., 2015; Stahlschmidt et al., 2017), bat activity in open agriculture may be even more strongly suppressed than recorded in our study.

4.2. Effects of agricultural management

Our most interesting finding is probably the outstanding value of grazed agroforestry systems for bats, even when compared with forests. This may be explained by a higher food availability in silvopastoral systems due to the presence of livestock (Fuentes-Montemayor et al., 2013; Ancillotto et al., 2017, 2021). Many insects are associated with dung, including dipterans (Davies, 1957; Steelman, 1976) and beetles (Merritt and Anderson, 1977) that provide important food resources for bats (Downs and Sanderson, 2010; Ancillotto et al., 2017, 2021) but also for other taxa including birds (Wilson et al., 1999). Interestingly, Ancillotto et al. (2017) and Downs and Sanderson (2010) found that bat foraging activity was higher in the presence of cattle than in the presence of only dung, suggesting that flies (Diptera) attracted to the livestock themselves represent important additional prey for foraging bats. The higher activity recorded in silvopastoral plots was mostly the result of the presence of several *Pipistrellus* species which are aerial hawkers feeding on flying insects foraging in relatively open areas (low tree densities and sparse understory cover). Other species, including *Myotis* spp., that forage in more cluttered environments, also showed a tendency to be more active in silvopastoral plots. *Rhinolophus ferrumequinum* is another example of a species that benefits from both a cluttered environment and the presence of livestock, feeding on dung-dwelling beetles (Jones, 1990) preferably in forests and semi-open habitats. Previous studies have also shown an elevated activity of *Pipistrellus* spp. in grazed sites (Downs and Sanderson, 2010; Fuentes-Montemayor et al., 2013; Costa et al., 2019; Ancillotto et al., 2017, 2021).

Differences in agricultural management may modulate the effects of agroforestry on bats. For example, high grazing intensity can reduce insect biomass (Jerrentrup et al., 2014), potentially lowering the food availability to bats. On the other hand, short swards may facilitate foraging for ground-gleaning species such as *Myotis myotis* (e.g. Zahn et al., 2006). Pesticide use can lead to food prey shortage and/or chemical exposure of bats, particularly in field crops and orchards, and turn such sites into “ecological sinks” (Russo

et al., 2024; Stahlschmidt et al., 2017). In our study, all agroforestry and respective control plots were grazed at low intensity and managed according to the standards of organic farming (EEC regulation No. 834/2007). In conventional animal husbandry, the use of anthelmintics can have particularly negative effects on the dung-associated fauna (De Souza and Guimarães, 2022). Organic grazing systems were thus shown to sustain higher insect abundance and diversity, which in turn can exert a positive effect on bat activity (Wickramasinghe et al., 2003, 2004; Ancillotto et al., 2023).

The lower bat activity in forests compared with silvopastoral systems is surprising since forests are known to represent one of the most important roosting and feeding habitats for bats (Mickleburgh et al., 2002; Fuentes-Montemayor et al., 2013; Heim et al., 2015; Russo et al., 2016; Frick et al., 2019). An explanation could be that apart from an increased prey availability, grazing with livestock helps to maintain an open understory and a lower tree density. This has been shown to benefit bats, as prey becomes more easily accessible, especially for ground-foraging bat species (Rainho et al., 2010) and aerial hawkers (e.g. *Pipistrellus* spp.) (Fuentes-Montemayor et al., 2013). Silvopastoral systems with their high structural diversity may resemble landscapes that were formerly maintained by mega-herbivores now extinct in Western Europe, such as bison and wild horses (Galetti et al., 2018). Such semi-open, savanna-like landscapes provide very different conditions from today's production forests with their closed canopies and may thus explain the high bat occurrence in silvopastoral systems. Our results are in line with those found by Obrist et al. (2011) who measured a higher bat species richness as well as a higher bat activity in managed orchards (grazed, pruned or mowed) with a less dense vegetation compared to unmanaged ones. Whilst bats benefit from the presence of livestock, the relationship may be mutualistic. Bats are known to play a crucial role in consuming hematophagous insects and can thus help prevent the transmission of pathogens to livestock (Downs and Sanderson, 2010; Ancillotto et al., 2017; Palmer et al., 2019). Bats have also been shown to regulate herbivorous and fungal pests in forests and agroecosystems (Böhm et al., 2011; Maine and Boyles, 2015; Charbonnier et al., 2021; Ancillotto et al., 2022; Maslo et al., 2022). Overall, bats support a wide range of ecosystem functions and services in agricultural areas, some of which may be economically significant (Boyles et al., 2011; Kunz et al., 2011; Maine and Boyles, 2015).

5. Conclusion

In conclusion, silvopastoral systems are highly beneficial for bat conservation. This is particularly true for systems in which old broadleaf trees are combined with livestock. Silvopastoral agroforestry met the requirements of a wide range of different bat foraging and hunting guilds including open/edge foragers and forest species. Given the current rise of interest in the benefits of agroforestry for biodiversity conservation, it is important to note that the benefits were strongest in systems with mature trees of > 50 years of age. This limits the conclusions that can be drawn on bat conservation from recently established agroforestry systems, and it indicates that systems with a short rotation of the tree component may be of limited conservation value. On the other hand, it emphasizes the importance of conservation of aged agroforestry stands. The results add to the growing evidence on the benefits of agroforestry systems to support farmland biodiversity and ecosystem service delivery through insectivory. Thus, agroforestry should be more widely adopted by farmers and supported with adequate policies. The role of agroforestry systems in supporting bat conservation may only be effective if they are extensively managed, with a low pesticide input and the absence of human induced threats (e.g. wind turbines and roads) in the vicinity.

Authors' contributions

ME, MHE, FH, JHNP, WS, JS and VR contributed to the study conception and design. ME, AW, JHNP, WS and JS collected the data. ME, VR, KN, AS and AW analyzed the data. ME led the writing, and ME, MHE, FH, JHNP, WS, JS and VR contributed to the finalization of the manuscript. All authors read and approved the final version of the manuscript.

Article impact statement

Agroforestry systems with old broadleaf trees positively affect bats and deserve more attention in conservation planning.

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Declaration of Competing Interest

We confirm having no conflicts of interests with them as well as no previous co-authored publications.

The work as submitted has not been published or accepted for publication, nor is being considered for publication elsewhere, either in whole or substantial part.

All authors and relevant institutions have read the submitted version of the manuscript and approve its submission.

All persons entitled to authorship have been so included.

The work is original and all necessary acknowledgements have been made.

The work conforms to the legal requirements of the country in which it was carried out, including those relating to conservation and welfare, and to the journal's policy on these matters.

Third party data sets used in this work are either publicly available for unrestricted reuse or permission for reuse has been obtained from the data owners

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Appendix A. Supporting information

Habitat characteristics and sampling dates of all studied plots (Supporting Table A1), results of post-hoc pairwise comparison showing and total bat activity differences (Supporting Table A2), feeding buzz and social call rate differences (Supporting Table A3) as well as the activity of different bat species in each sampled plot (raw data) (Supporting Table A4) are available as supporting information in the online version of the article at the publisher's website. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2024.e03369](https://doi.org/10.1016/j.gecco.2024.e03369).

Data availability

Data will be made available on request.

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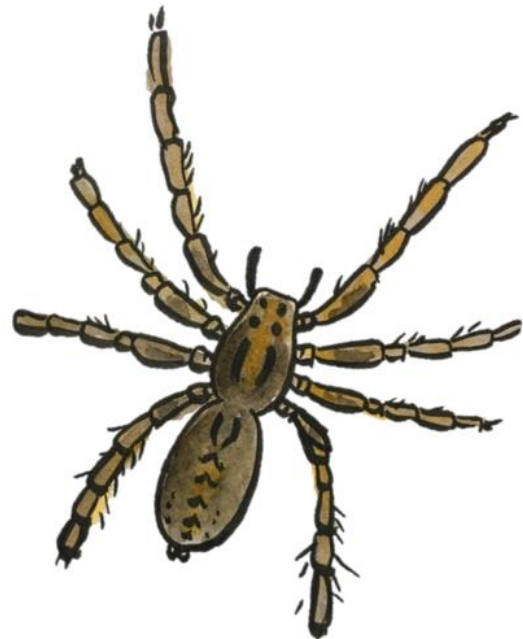
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CHAPTER IV

THE POTENTIAL OF AGROFORESTRY AND SMALL FIELDS TO ENHANCE GROUND-DWELLING SPIDERS

Manon Edo, Felix Herzog, Gerardo Moreno, Rodrigo Olave, Alice Ripamonti, Verena Rösch, Will Simonson, Lorenzo Gabriele Tramacere, Olivier Villepoux and Martin H. Entling



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

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0) 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 areas. Our findings reveal that agroforestry supports species from both open and forested habitats, contributing to landscape-scale biodiversity by fostering unique spider assemblages. Alpha diversity was higher in silvopastures than in forest, 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 habitat types. High 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 results highlight the potential of combining productive agricultural systems with different conservation strategies to restore biodiversity in agricultural landscapes. A mosaic of small fields with diverse land uses, combined with seminatural habitats and structurally heterogeneous productive systems like agroforestry, can enhance biodiversity and ecosystem resilience.

1) Introduction

Over the past decades, arthropod diversity and abundance have declined drastically on a global scale (Hallmann 2017; Seibold et al. 2019; van Klink et al. 2021). One of the main reasons for this ongoing decline is habitat loss, primarily caused by agricultural systems simplification and homogenization. Agroforestry systems, which deliberately integrate trees with agricultural crops and/or pastures, have the potential to reconcile food production with environmental benefits and biodiversity conservation (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), bats (Edo et al. 2025), and arthropods (Boinot et al. 2019, 2020; Pardon et al. 2019; Kay et al. 2019b; Mc Adam et al. 2007; Peng et al. 1993; Bentrup et al. 2019).

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). They occur in high diversity and density across all European ecosystems (Foelix 2011; Nyffeler 2000) and are highly sensitive to environmental changes, 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). 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. 2015; 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 22 agroforestry systems (8 silvoarable and 14 silvopastoral) and 44 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, cultivated vs grazed ones.

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 include mainly generalist species that rely on both forested and open 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 field—will be higher in agroforestry systems than in other field and habitat types. We further hypothesize that species richness will be higher in small fields than in larger ones due to spillover and resource complementation between habitats.

2) Material and Methods

2.1) 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 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 agroforestry plot and were located in the near surroundings to minimize the variation of e.g. climate, soil, and the surrounding landscape (**Fig. 1**). In total, 13 open pastures, 15 forests and 2 orchards were sampled as controls for the silvopastoral plots ($n=14$) and 6 crop fields, 6 forests and 4 orchards were sampled as controls for the silvoarable plots ($n=8$). Fruit or nut 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 Food and Agriculture Organization of the United Nations 2018). The control orchard and forest plots contained trees of approximately the same age as those in the corresponding agroforestry plots. Additionally, 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 $\pm$ 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**).

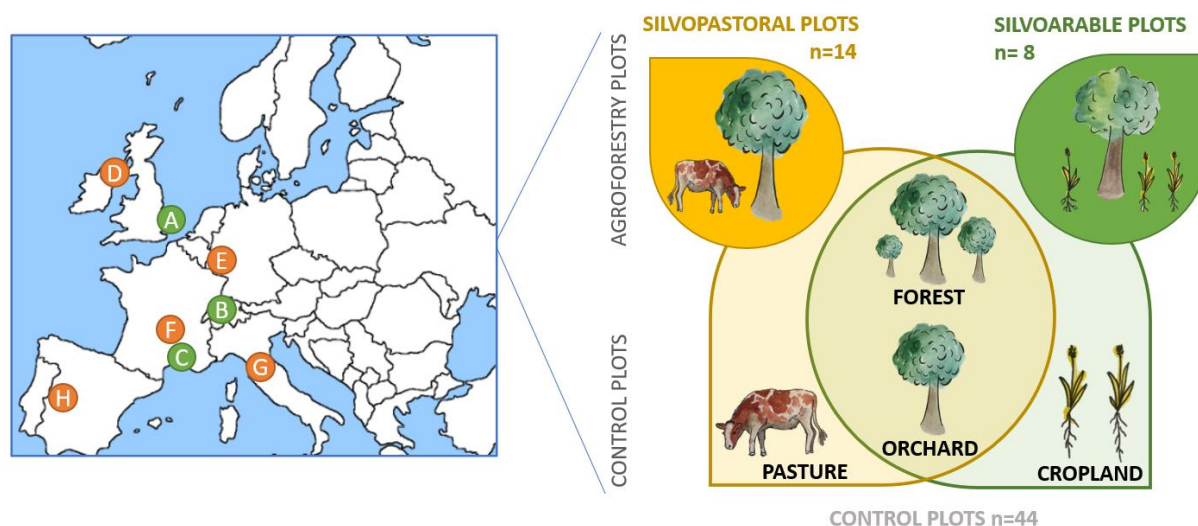


FIGURE 1 Geographic location of the silvoarable (A-C) and silvopastoral (D-H) study sites.

● = silvoarable sites: A = Wakelyns (UK), B = Möhlin and Sursee (CH), C = Restinclières (FR)

● = 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 to 3 agroforestry (either silvopastoral or silvoarable) plots were sampled. In addition to each agroforestry plot, 2 to 3 control plots were sampled.

2.2) 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 and transects were usually oblique to the tree rows to ensure the 20m transect length between the centre of the alley and the tree line (**Fig. 2**). In total 264 pitfall traps were placed across the 66 sampled plots. Pitfall traps were filled with 100ml of propylene glycol mixed with tapwater (1:2), odor-free detergent to break the surface tension and a bitter agent to avoid the destruction of the traps by large mammals (e.g. wild boar, deer), and exposed for 10 days in each plot. 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 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).

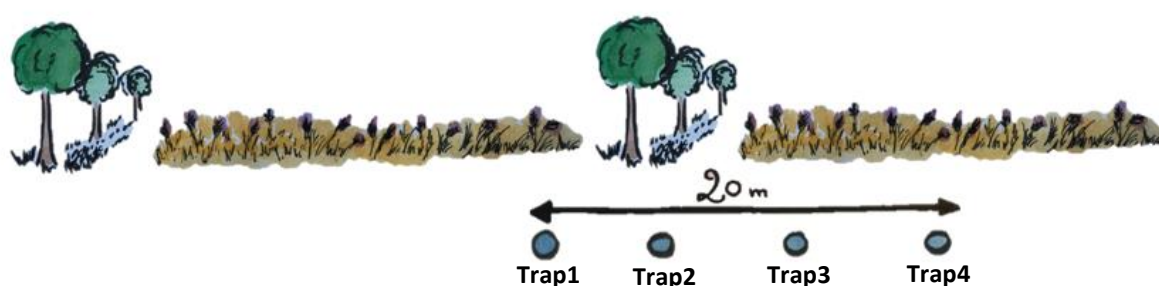


FIGURE 2 Equidistant placement of the pitfall traps on the 20 m transect. In plots with trees, trap 2 was always placed under a tree (1 m from the tree trunk) and trap 4 in the middle of the crop or pasture alley. Traps 1 and 3 are placed in the crop or pasture alley.

2.3) 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, a partial redundancy analysis (pRDA) based on the number of sampled individuals per species and per plot over the season was performed. The pRDA was conducted with land-use type (in the following referred to as “Habitat”) as explanatory variable and country 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). A permutation test with 9999 permutations was used to determine the significance of the results (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 1949) were computed for each plot, using the PAST software (Hammer 2020) (see **Supplementary Table S1**). Linear mixed-effect models were fitted (R package *lme4*, function *lmer*, Bates et al. 2015) with habitat type set as explanatory variable and “site” as a random factor, due to the nested design of the study (equations: $\text{lmer}(\text{SpR} \sim \text{Habitat} + (1|\text{Site}))$ and $\text{lmer}(\text{Inv-Simpson} \sim \text{Habitat} + (1|\text{Site}))$). 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: $\text{lmer}(\text{SpR} \sim \log(\text{Size}) + \text{Habitat} + (1|\text{Site}))$). 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: $\text{lmer}(\text{SpR} \sim \text{Habitat} + \text{Number of traps} + (1|\text{Site}))$). As the results were highly similar, we show the results without accounting for missing traps.

To assess differences in β -diversity within and 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, β -diversity (β_{jac} total Jaccard dissimilarity) was partitioned into two components: the turnover (β_{jtu} species replacement) and nestedness (β_{jne} species loss or gain due to differences in species richness) (R package *betapart*, function *beta.pair*, Baselga, 2010). The objective of this analysis being to determine the species turnover among plots and among habitats, independent of richness differences, 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) ($\text{aov}(\beta_{jac} \sim \text{Country} + \text{Habitat2})$ (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 §3.1 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).

3) Results

3.1) 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 ($F = 1.72$, $p = 0.0001$). Habitats explained 9.5% of the total variance after controlling for country effect (explaining 31.8% of the variance). Spider communities were clearly separated across different habitat types, with spider communities in agroforestry having an intermediate position, suggesting that they contain species from the four other habitat types (**Fig. 3**). The RDA also highlights that silvopastures show a higher dispersion and thus a more variable species composition than silvoarable systems.

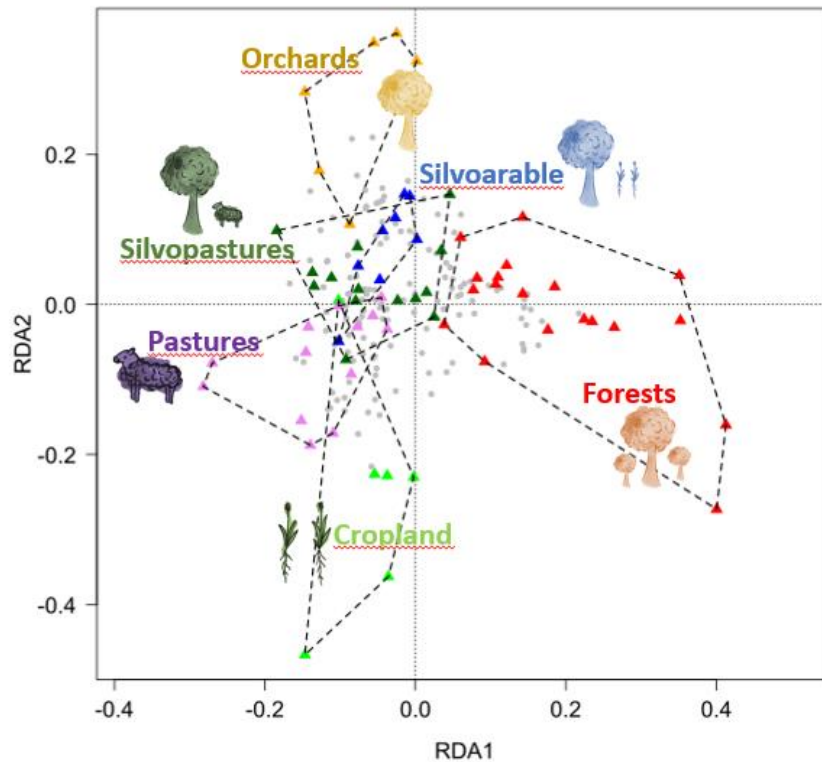


FIGURE 3 Composition of the spider communities in the different habitat types (silvopastures, pastures, orchards, croplands and silvoarable systems), analysed with redundancy analysis. Grey dots indicate spider species, and dashed lines represent minimum convex polygons around habitat types with the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

3.2) 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**). 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**). 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.

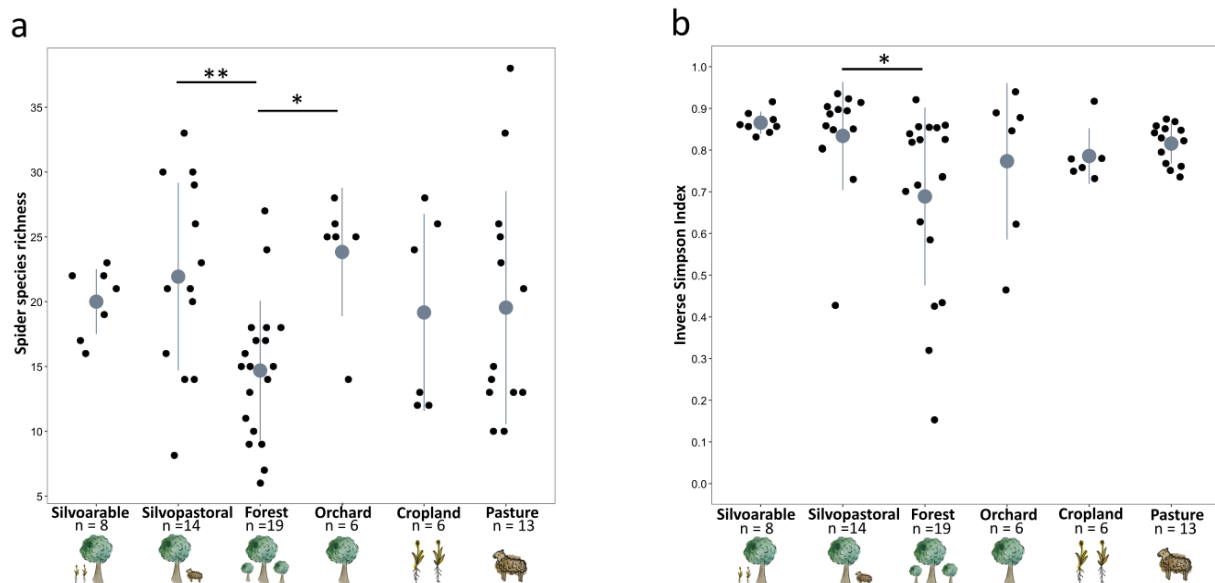


FIGURE 4 a) Spider species richness (mean) **b)** Inverse Simpson index (mean) (referred as Simpson diversity) per habitat type. Significance levels: * $p < 0.05$, $0.001 < **p < 0.01$. See **Supplementary Table S4** for the detailed results of species richness and Simpson diversity in the different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

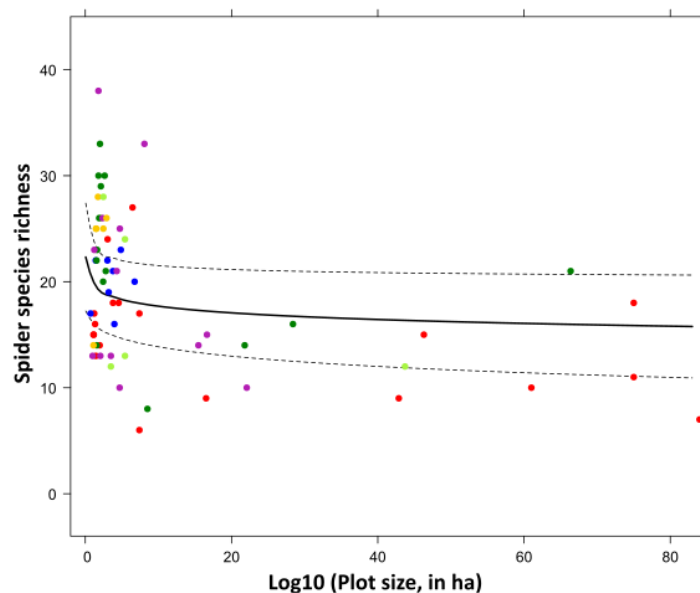


FIGURE 5 Effect of plot size (log10) in hectares (ha) on spider species richness across habitat types: silvoarable (dark blue dots) and silvopastoral (dark green dots) agroforestry systems, forests (red dots), orchards (yellow dots), cropland (light green dots) and pastures (purple dots).

3.3) β diversity (turnover)

Species turnover between plots (β_{jtu}) differed significantly between countries ($F = 3.62$, $p = 0.019$). However, there were no significant differences in between-plot species turnover between 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**).

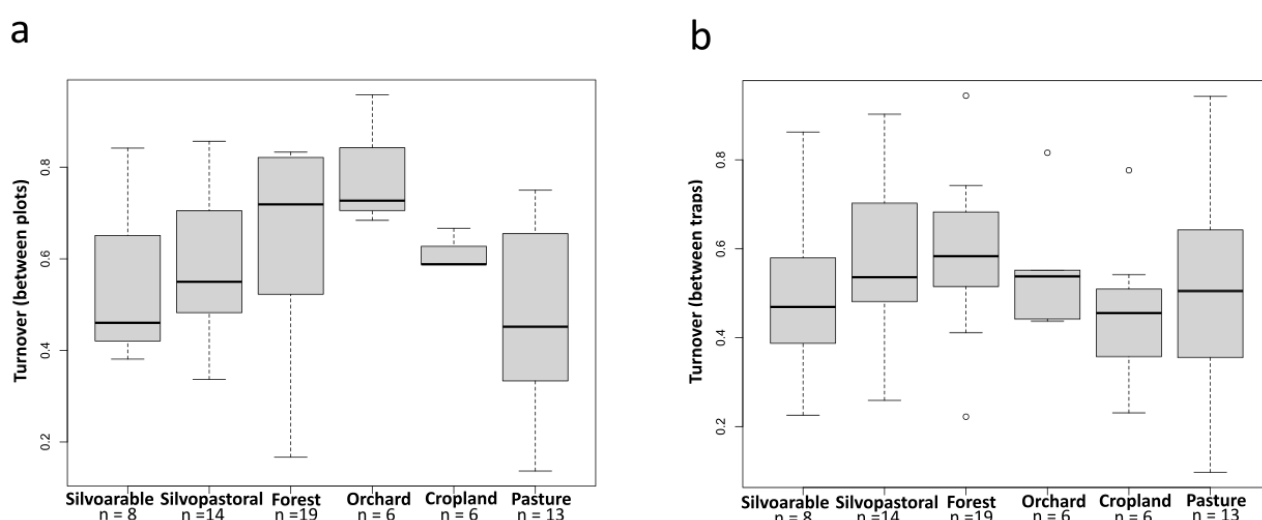


FIGURE 6 Median species turnover (β_{jtu}) calculated via pairwise comparison of the spider communities **a**) between plots of the same habitat type in each country **b**) between traps of a same plot.

3.4) Indicator species

The indicator species analysis showed a strong association of the two species *Trochosa* and *Diplostyla concolor* with silvoarable plots (**Table 1**). By contrast, no indicator species was 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*, *Hahnian nava*, *Pardosa hortensis* and *Micrargus subaequalis* were indicator species for orchards.

TABLE1 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 as well as those which had a total abundance (across all plots) higher than five individuals are listed in the table.

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

4) Discussion

According to our hypothesis, spider communities in agroforestry systems comprise 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 fields and between traps within fields 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.

4.1) 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 forested 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 open-land 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. 2020; 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. 2008; 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. 2008; Birkhofer et al. 2015), 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 open-land 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 fields 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.

4.2) 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 fields—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). Matevski et al. (2024) reported higher ground-dwelling spider abundance in silvoarable systems compared to cropland, while a decrease of the grazing intensity, which promotes higher and more structured vegetation, has been linked to an increase in spider species richness in grasslands (Horvath et al. 2008). 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. 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 plots and other habitat types. The greater structural heterogeneity of agroforestry plots compared to more homogeneous control fields 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 fields 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 confirming our results, Lüscher et al. (2014) in their 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 2015; Šálek et al. 2018; Sirami et al. 2019; Tschardt et al. 2021;). Small field size can facilitate spider immigration and spillover from field edges and neighboring habitats (Schmidt et al. 2008; Schmidt and Tschardt 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.

4.3) Conclusions/Management implications

Agroforestry systems create an ecological setting where open and wooded habitats coexist in close proximity—an uncommon feature in many 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 significantly enhance overall biodiversity at the landscape scale by hosting distinct spider communities. Thus, agroforestry seems an ideal component of crop 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 specific management practices and vegetation structures (e.g., wooded, open, grazed, and non-grazed areas). This study underscores the need to enhance structural complexity at both field and landscape scales, as well as over time, to effectively support ecosystem resilience and biodiversity conservation (Tscharntke et al. 2012; Gonthier et al. 2014; Sirami et al. 2019). When appropriately managed, agroforestry systems can restore heterogeneity in European agricultural landscapes, bolstering ecosystem resilience to disturbances while supporting essential ecosystem services.

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 across trophic levels and ecosystem functions in agricultural landscapes.

Appendix

Table S1: Habitat characteristics of all studied sites

Table S2: Spider abundance per habitat type

Table S3: Results of linear mixed effects models showing total spider abundances differences between habitats

Table S4: Results of linear mixed effects models showing total species richness (a) and Simpson diversity (b) differences between habitats

Author's contribution

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.

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Statements and Declarations

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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

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CHAPTER V
GENERAL DISCUSSION AND OUTLOOK
Manon Edo



Agroforestry for biodiversity conservation: emphasizing the role of multi-taxa approaches

Based on biodiversity data collected across more than 60 agroforestry and control plots in eight European countries, **Chapters II, III, and IV** provide evidence that both silvoarable and silvopastoral systems hold strong potential for supporting the conservation of birds (**Chapter II**), bats (**Chapter III**), and ground-dwelling spiders (**Chapter IV**) in European farmlands. Across **all chapters**, we observed taxon-specific responses to field variables, such as within-field heterogeneity (**all chapters**), tree type and age (**Chapter III**), presence of grazing livestock (**all chapters**), or field size (**Chapter IV**). These environmental variables differently shaped the diversity and community structure of each animal group and the variability of responses may be explained by differences in ecology among taxonomic groups (Tscharntke et al., 2005; Turtureanu et al., 2014).

As shown in **Chapter II**, bird diversity was higher in both silvoarable and silvopastoral fields compared to open agricultural land, highlighting the benefits of within-field structural heterogeneity provided by agroforestry systems for birds. This positive response can likely be explained by the greater niche availability offered by these systems, which supports diverse foraging and nesting opportunities for birds (Söderström et al., 2001). The within-field heterogeneity of agroforestry systems supported not only birds but also bats. Interestingly, as shown in **Chapter III**, the presence of a single element contributing to structural complexity—such as either trees or livestock alone—seemed to have a limited effect, with bat activity showing no significant differences between silvoarable systems and conventional cropland, or between pastures and cropland. However, **Chapter III** highlighted the importance of livestock grazing in combination with woody elements for supporting bat activity as silvopastoral systems had the strongest positive effect on bat activity compared to silvoarable systems, pastures, or forests. Tree characteristics strongly affected bat activity which was notably higher in stands with old and deciduous trees compared to those with younger or coniferous trees. These patterns can likely be explained by prey and shelter availability. Trees lines can protect bats from wind and predators and favour their echolocation and flight (Downs and Racey, 2006; Verboom and Huitema, 1997). Moreover, old deciduous trees and grazed sites are known to support higher insect abundance, which in turn attracts foraging bats (Ancillotto et al., 2017; Russo et al., 2016). Given their very high metabolic rate (Jones et al., 2009; Russo et al., 2021), bats are highly dependent on abundant and reliable food sources. Their ability to travel long distances—up to 30–40 km from their roosts (Arthur and Lemaire, 2015)—enables them to selectively exploit areas with higher prey density. This high mobility and dependence on prey-rich and safe habitats may explain the strong positive response of bats to specific field parameters that enhance food availability, such as the presence of both trees and grazing livestock in silvopastoral systems.

In contrast to bats, birds (**Chapter II**) appear to be less selective in their dietary requirements and are not strictly dependent on arthropods. Many bird species are capable of feeding on both seeds and invertebrates, although the importance of invertebrates in their diet tends to increase during the breeding

season (Holland et al., 2006). Unlike arthropod activity—which can fluctuate greatly depending on climatic conditions—seeds provide a more stable food resource throughout the year (Holland et al., 2006). This broader dietary niche may explain the higher abundance and diversity of birds, observed in both silvoarable and silvopastoral systems compared to open agricultural land (**Chapter II**). For birds, the structural heterogeneity created by woody elements may offer sufficient foraging, shelter and roosting opportunities to make these habitats attractive. Bats, by contrast, due to their more specialized diet and reliance on high prey densities, may preferentially exploit grazed agroforestry areas where prey availability is particularly high.

In **Chapter IV**, in contrast to birds and bats, spider diversity showed only few differences between habitat types, with similar species richness observed in all systems except forests, where lower values likely resulted from reduced sampling coverage. Spiders are among the most diverse terrestrial predators in Europe (Foelix, 2011) and, like birds and bats, are sensitive to agricultural intensification, habitat simplification and environmental change (Branco and Carodoso, 2020). However, unlike highly mobile birds and bats that can relocate when conditions become unsuitable (Jones et al., 2009), spiders have a limited dispersal and must cope with local changes. Their ability to endure food scarcity for extended periods and to quickly recolonize disturbed areas from nearby habitats as well as their high reproduction rates contributes to their resilience and help them persist across various environments (Schmidt et al., 2008). The high diversity of spider species has facilitated their adaptation to extreme conditions; for instance, some species—referred to as agrobiont spiders—are particularly well adapted to survive in highly disturbed agricultural landscapes (Mestre et al., 2018). This adaptability and ecological diversity likely explain the relatively similar levels of spider diversity we observed across all habitat types. Although spider diversity was not directly influenced by within-field parameters, **Chapter IV** showed that community composition varied significantly across habitats, highlighting the role of field structure and microclimatic conditions at small spatial scales in shaping ground-dwelling spider assemblages (Lüscher et al., 2014). Similarly, **Chapter II and III** revealed that bird and bat communities differed between the habitat types and that communities in agroforestry systems were shaped by their structural heterogeneity. Together, these chapters demonstrated that agroforestry systems support the coexistence of species associated with both open-land and wooded habitats within the same area.

Together, **Chapters II, III, and IV** showed that a wider implementation of agroforestry in European farmland could simultaneously benefit birds, bats and spiders and may also benefit other taxa, providing valuable habitats for them. However, **Chapters II, III, and IV** revealed distinct benefits of agroforestry systems for each group. These taxon-specific responses to habitat structure and environmental variables highlight the importance of considering multiple taxa with variable ecological traits, spatial ranges, within-taxa species richness, and life strategies when designing conservation strategies (Lüscher et al., 2014).

From field to landscape: expanding the scale of biodiversity conservation in agroecosystems

Chapters II, III, and IV of this thesis demonstrated that increasing within-field heterogeneity through agroforestry benefits birds, bats, and spiders. However, the role of agroforestry probably extends beyond field-scale benefits, contributing significantly to biodiversity at the landscape level.

Notably, **Chapter II** revealed significantly higher bird diversity in agroforestry systems within both temperate and Mediterranean regions compared to other habitat types. In contrast, temperate open agricultural fields (croplands and pastures) recorded no bird presence. **Chapter III** also revealed higher bat activity in silvopastoral systems compared to pastures and croplands. Moreover, all chapters reveal that agroforestry systems can host unique communities of birds, bats, and spiders, comprising both species associated with open habitats, and those associated with wooded habitats. These results highlight the critical role of agroforestry in enhancing biodiversity at landscape-scale—a key determinant of local biodiversity and ecosystem resilience (Tscharntke et al., 2005). Interestingly, **Chapter II** confirms this relation between landscape and local richness: in agroforestry systems embedded in intensively managed temperate landscapes, only generalist and woody-habitat bird species were recorded, which can probably be explained by the biotic homogenization in those regions (Ekroos et al., 2010; Reif and Hanzelka, 2020). Inversely, Mediterranean agroforestry systems embedded in extensively managed landscapes supported species of both open and wooded environments (Kleijn et al., 2009). These regional differences confirm the hypothesis that conservation effectiveness varies with landscape context (Tscharntke et al., 2005). However, **Chapter II** demonstrated the potential of agroforestry as a conservation strategy to support bird diversity in both simple (temperate) and complex (Mediterranean) landscapes. These benefits likely stem from agroforestry's structural complexity, which increases ecosystem resilience and reduces reliance on external inputs, while simultaneously expanding permanent semi-natural habitats—both key strategies for biodiversity conservation in farmland (Tscharntke et al., 2005).

Agroforestry systems also provide important ecological corridors. Trees and shrubs in these systems, particularly in low-disturbance settings, enhance habitat connectivity and support gene flow among wildlife populations, increasing resilience to climate change and other disturbances (Ekroos et al., 2010; Garibaldi et al., 2021; Manning et al., 2006). For instance, bats are known to utilize linear vegetation features—such as hedgerows and tree lines—as movement corridors, facilitating navigation and foraging across agricultural landscapes (Verboom & Huitema, 1997). Moreover, benefits observed at the field scale (e.g., pest control, erosion prevention) may extend into adjacent fields, amplifying their positive landscape-level effects (Matson et al., 1997). It is important to note that silvoarable and silvopastoral agroforestry systems—examined in **Chapters II, III, and IV**—are not the only options for reintegrating semi-natural habitats into agricultural landscapes. Other agroforestry features where trees are primarily located at field edges, such as field boundaries, hedgerows, and riparian buffers, are

widespread across northwestern Europe and their wider implementation would also benefit biodiversity (Chávez et al., 2025; Morelli, 2013; Rubio-Delgado et al., 2024).

Additional sustainable practices and management strategies, including polycultures, crop-livestock integration, rotational grazing, conservation agriculture, soil, water and integrated pest and nutrient management, can also improve biodiversity and ecosystem services (MacLaren et al., 2022; Pretty & Bharucha, 2014; Ramankutty et al., 2018; Tamburini et al., 2020). In agroforestry systems, optimizing grazing management, tree pruning, tree density and species selection were shown to greatly influence both productivity and biodiversity (Matson et al., 1997; Rigueiro-Rodríguez et al., 2009). Beyond the composition of agricultural fields, management strategies that influence field configuration within the landscape play a critical role in shaping biodiversity outcomes (Fahrig et al., 2011). As demonstrated in **Chapter IV**, smaller fields can enhance ecological connectivity and support higher ground-dwelling spider diversity. These findings underscore the importance of proximity to diverse source habitats, as well as the value of heterogeneous landscapes with smaller field sizes in promoting biodiversity (Fahrig et al., 2015; Gavish et al., 2012; Šálek et al., 2018; Sirami et al., 2019). This is particularly relevant for species with low dispersal capacities, as landscape complexity facilitates recolonization and population recovery following disturbances (Schmidt et al., 2008; Tscharntke et al., 2005). Moreover, an increased proportion of smaller fields within a landscape is often associated with a higher total length of semi-natural boundaries—such as hedgerows, grassy margins, or tree lines—which have been shown to significantly enhance biodiversity in adjacent crop fields (Concepción et al., 2012).

Each of the aforementioned practices and management strategies contribute to the provisioning of key regulating and supporting ecosystem services—such as pest control, pollination, and soil stabilization—thereby maintaining agricultural productivity and promoting long-term sustainability. By reducing reliance on external inputs that can degrade ecosystem health, they enhance the resilience of agroecosystems. While agroforestry systems alone can significantly support these processes, the combination of multiple sustainable practices implemented across the landscape scale would further strengthen agroecosystem resilience and biodiversity conservation.

Importantly, because taxonomic groups differ in their responses to environmental variables and habitat structure, the implementation of a heterogeneous landscape mosaic is essential for effective multi-taxa conservation and the development of sustainable agricultural systems (Fahrig et al., 2015; Tscharntke et al., 2005). This was confirmed by the community composition analyses presented in **Chapters II and III**, which revealed substantial variation in species assemblages across forests, agroforestry systems, orchards, and open agricultural fields. Maximizing biodiversity at the landscape scale thus requires a combination of habitat types and successional stages, incorporating open and wooded areas, large and small patches, and both cultivated and uncultivated zones. As demonstrated in this thesis, biodiversity benefits from the coexistence of open and wooded habitats not only at the field scale, but also at the landscape scale. Agroforestry systems, by embedding trees and semi-natural elements within productive

farmland, have strong potential to support this ecological diversity without compromising yield (Smith, 2010; Torralba et al., 2016).

Study limitations and recommendation for future research

These studies underscore the potential of agroforestry systems to support biodiversity at both field and landscape scales. However, our research primarily focused on field-scale effects. To refine conservation strategies and maximize biodiversity benefits, further research is needed to explore how landscape composition and configuration influence agroforestry's ecological outcomes across a wider range of taxa (Lüscher et al., 2014; Fahrig et al., 2011). Understanding how surrounding land use modulates the benefits of agroforestry—and conversely, how agroforestry influences adjacent land use—is crucial. Agroforestry systems may provide advantages that extend beyond individual fields, supporting at landscape-scale, a more diverse species pools, enhancing ecological connectivity, and delivering essential ecosystem services such as pest control and pollination, which are vital for the resilience of agroecosystems (Garibaldi et al., 2021; Rusch et al., 2016). Assessing the effects of agroforestry systems on a broader range of ecosystem services at field and landscape scale would also broaden our understanding of their role in promoting sustainable intensification (Jose, 2009).

As demonstrated in these studies, different taxa respond variably to agroforestry practices. Even closely related taxa may respond differently to environmental conditions and management practices (Kotze & Samways, 1999; Turtureanu et al., 2014; Yong et al., 2018). Expanding research to include other organisms—such as herbivorous arthropods, plants, microorganisms, or highly specialized parasitoid wasps would provide a more holistic understanding of how agroforestry can support biodiversity and enhance ecosystem functioning (Tscharntke et al., 2005). Importantly, future studies should examine the impact of agroforestry on open landscape specialists, which may be negatively affected by the integration of trees into open farmland (Graham et al., 2017). In our study, we recorded the presence of open landscape specialists such as larks and corn buntings in Mediterranean agroforestry systems and adjacent open agricultural control fields. However, to more accurately assess potential negative effects on these species, long-term monitoring over multiple years is essential (Graham et al., 2017).

A limitation of these studies was the relatively small sample size of silvoarable fields, all of which contained young trees, as such systems are still limited in Europe, with many alley-cropping systems being relatively new (Dupraz & Liagre, 2008). Moreover, all agroforestry systems we studied were managed organically. Investigating a broader range of silvoarable and silvopastoral systems, particularly those featuring older, more mature trees and diverse management strategies, would help refine our findings. Management practices are known to significantly influence farmland biodiversity outcomes at both field and landscape scale (Meier et al., 2022). Incorporating additional agroforestry types—such as

those featuring older, more mature trees and diverse management strategies, would help refine our findings. Management practices are known to significantly influence farmland biodiversity outcomes at both field and landscape scale (Meier et al., 2022). Incorporating additional agroforestry types—such as hedgerows, windbreaks, and riparian buffers, where trees are primarily located along field edges—into future European-wide studies would deepen our understanding of the biodiversity impacts of agroforestry. While our study focused on silvoarable and silvopastoral systems, these edge-based agroforestry practices are still the most widely implemented across European farmland. (Rubio Delgado, 2024).

Conclusion: challenges to large-scale implementation of agroforestry

Despite the recognized ecological benefits of agroecological practices such as agroforestry, their adoption remains limited in Europe. Despite agroforestry being acknowledged as a sustainable agricultural practice (FAO & ICRAF, 2019) and its well-documented potential to enhance biodiversity, ecosystem services, and agricultural resilience (Fagerholm et al., 2016; Jose, 2009), the area covered by silvopastoral and silvoarable systems declined between 2009 and 2018 (Rubio-Delgado et al., 2023). This decline reflects long-term trends dating back to the Green Revolution and is driven by several socio-economic and environmental factors: increased mechanization, reduced outdoor grazing, aging tree stands, farm abandonment, rural depopulation, and climate-induced water scarcity (Eichhorn et al., 2006; Rodriguez-Rigueiro et al., 2021; Rubio-Delgado, 2023). Critically, wider adoption of agroforestry continues to be hampered by policy barriers: current agricultural frameworks, particularly those shaped by the European Union's Common Agricultural Policy (CAP), have historically incentivized simplified, large-scale monocultures at the expense of diversified systems like agroforestry (Graves et al., 2009; Nerlich et al., 2013). Political measures supporting more standardized fruit production systems has for example reduced intercropped and grazed orchards (Eichhorn et al., 2006). Many subsidy schemes and land classification systems do not adequately recognize or reward the multifunctionality of agroforestry systems, leading to uncertainties or financial disincentives for farmers who might otherwise adopt these practices (Eichhorn et al., 2006; Santiago-Freijanes et al., 2018). Moreover, reforestation and afforestation programs, although well-intentioned for climate mitigation, often prioritize tree planting over the maintenance of traditional silvopastoral systems, resulting in landscape closure and biodiversity loss, particularly in Mediterranean regions (Santiago-Freijanes et al., 2018). Institutional fragmentation, wherein agroforestry falls between forestry and agriculture sectors without clear policy responsibility, also complicates its promotion (Fagerholm et al., 2016). Crucially, the lack of targeted policy support, technical and practical knowledge and support about agroforestry practices among both farmers and policymakers as well as institutional barriers remain significant obstacles to broader agroforestry adoption (Graves et al., 2009; Nerlich et al., 2013).

policies that encourage the adoption of agroforestry by recognizing its multifunctional benefits for biodiversity, climate resilience, and farm productivity; (2) aligning agricultural and forestry policies to overcome the historical separation of these sectors, ensuring cohesive regulations that facilitate integrated land management; (3) providing financial incentives and subsidies (e.g., payments for ecosystem services) to support farmers in establishing and maintaining agroforestry systems; and (4) enhancing training, advisory services, and knowledge exchange to equip farmers, land managers, and policymakers with practical skills and a deeper understanding of agroforestry's benefits and management (Pantera et al., 2021; Smith et al., 2012).

Current EU agri-environment schemes that mostly focus on local-scale changes have to integrate broader spatial scales and should operate across field, landscape, national, and global scales, explicitly promoting the integration of semi-natural habitats within productive farmland (Garibaldi et al., 2021; Kleijn & Sutherland, 2003; Šálek et al., 2018; Torralba et al., 2016; Tscharntke et al., 2005). However, the sensitivity of certain open-habitat species underscores the importance of careful site selection when establishing agroforestry systems, as tree planting in inappropriate locations can inadvertently harm biodiversity. To minimize negative impacts, new agroforestry efforts should prioritize areas of intensively managed farmland—where biodiversity is typically low—while avoiding high-value conservation areas such as species-rich grasslands (Graham et al., 2017). Conservation must operate across field and landscape levels and also include "working landscapes"—areas under active agricultural use but not currently considered in conservation planning (Garibaldi et al., 2021). We urgently have to move beyond the dichotomy between cultivated and natural systems: both are deeply interconnected and should be managed as part of a unified socio-ecological system (Tscharntke et al., 2012). Conservation should not be confined to the remaining 5% of protected wilderness (in national parks or reserves) but extended into agricultural areas, which cover nearly 40% of the Earth's surface and provide habitat for approximately half of Europe's species (Foley et al., 2011; Kristensen, 2003; Kleijn & Sutherland, 2003). Set-asides and native habitats should cover at least 20% of agricultural landscapes to sustain essential ecosystem services, including pollination, pest control, and biodiversity conservation (Garibaldi et al., 2021; Tscharntke et al., 2011). A diverse habitat mosaic that supports species with varying ecological requirements is the most reliable path to sustainable land use (Tscharntke et al., 2005).

Agroforestry holds significant potential to meet these challenges. Its implementation can increase semi-natural habitat cover in agricultural landscapes, support biodiversity, and maintain yields, contributing to food security and rural well-being. By aligning agricultural production more closely with nature, agroforestry fosters synergies rather than trade-offs between ecological and agronomic goals.

Toward a systemic shift in agriculture

Ultimately, the transition toward sustainable agriculture requires collaboration among farmers, scientists, industry, policymakers, and civil society (Matson et al., 1997). It must integrate all three dimensions of sustainability: social, economic, and environmental (Helfenstein et al., 2020). Field- and landscape-level improvements are necessary, but not sufficient. Transformations must also span the entire food system—from production and processing to consumption—addressing issues such as food waste and dietary choices (Ingram, 2011; Ramankutty et al., 2018; Tilman and Clark, 2014). Only by integrating ecological principles into all levels of agricultural planning and decision-making can we ensure a resilient and sustainable future for both people and nature.

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APPENDIX



SUPPLEMENTARY MATERIALS

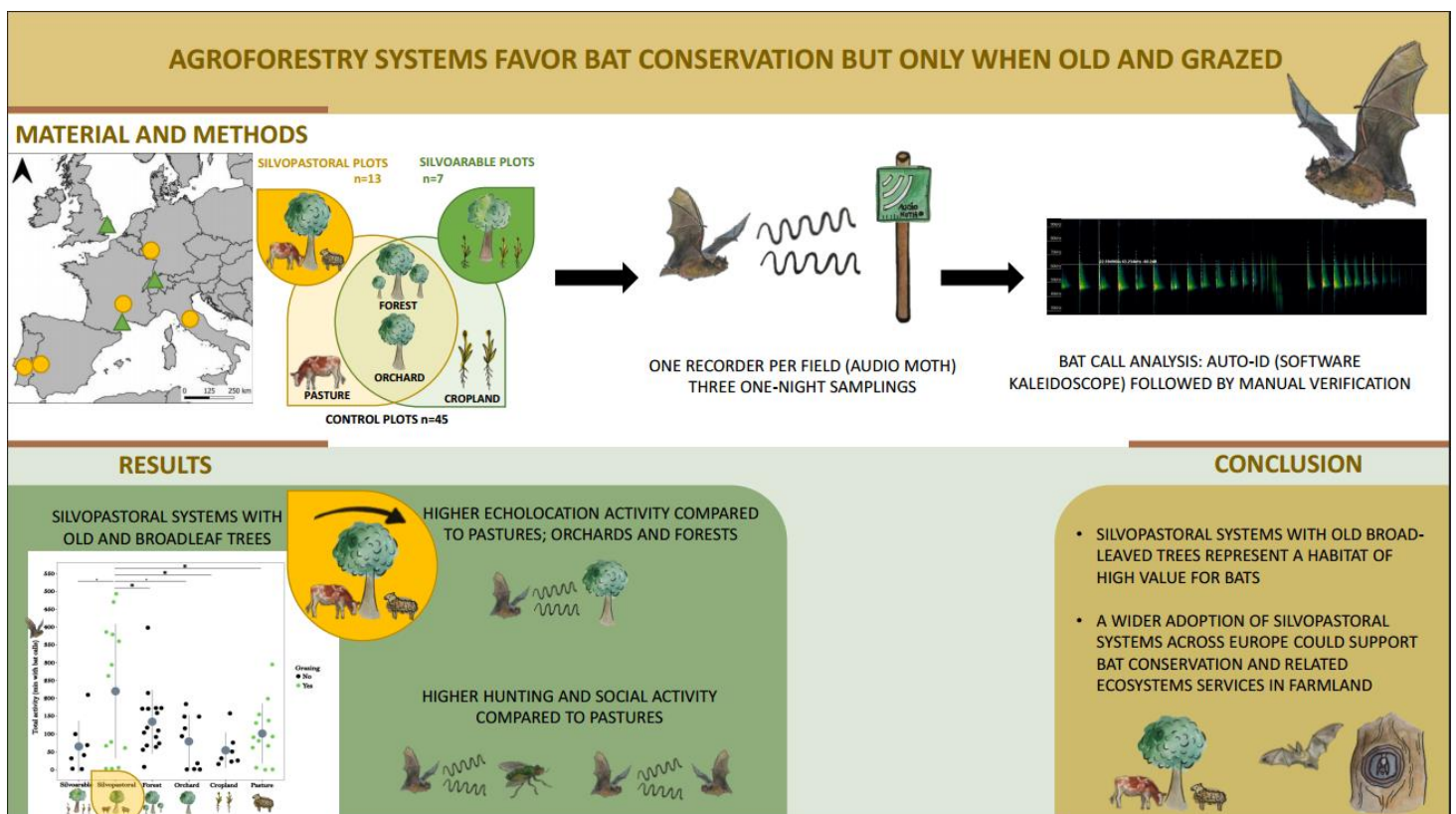
CHAPTER II

Supplementary tables and figures associated with this chapter are available in the online version at <https://doi.org/10.1007/s13593-023-00936-2>

CHAPTER III

Supplementary tables and figures, along with the high-resolution graphical abstract associated with this chapter, are available in the online version at <https://doi.org/10.1016/j.gecco.2024.e03369>

Graphical abstract:



SUPPLEMENTARY MATERIALS

CHAPTER IV – SUPPLEMENTARY TABLES AND FIGURES

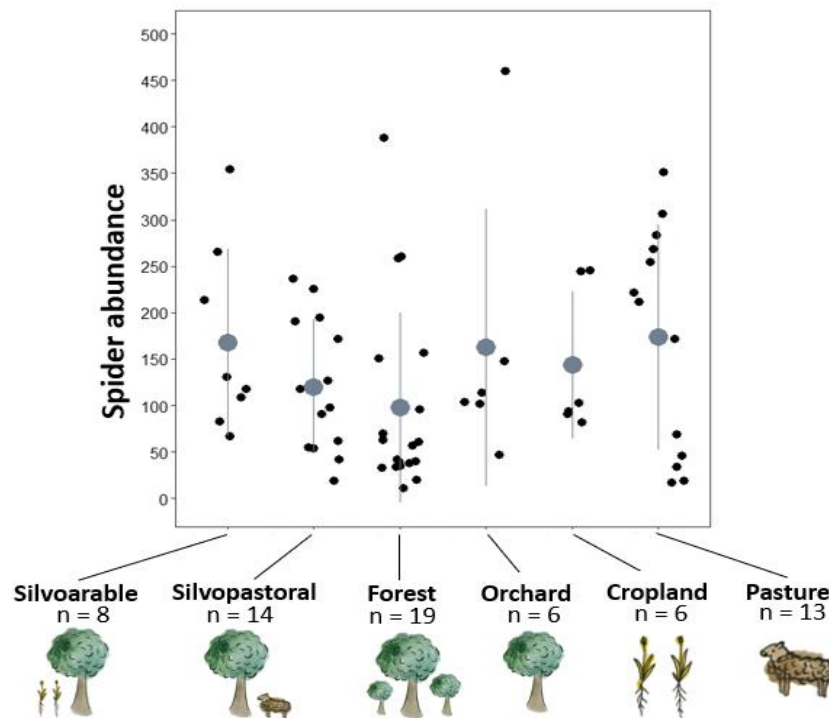
CHAPTER IV **Table S1** Habitat characteristics of all studied sites (n=66) located in eight different European countries and species richness of spiders. Agroforestry sites (AF, n=22) were either silvo-arable (SA) or silvo-pastoral (SP) systems. For silvo-arable systems, control fields were a cropland (A), a forest (F) and/or an orchard (O). For silvo-pastoral systems, control fields were a pasture (A), a forest (F) and/or an orchard (O).

Field_ID	Country	Location	Habitat type	Management (Or=Organic; C=Conventional)	Agroforestry system (SA=silvo-arable- SP=silvo-pastoral)	Livestock used (C=cattle-S=sheep)	Stocking density (Large livestock units-ha)	Last grazing date	Tree age	Intra-row distancen (m)	Alley-width (m)
DEBa_A1	DE	Odernheim-am-Glan	A	Or	-	C	0.8	May-21	NA	-	-
DEBa_A2	DE	Odernheim-am-Glan	A	Or	-	C	0.8	May-22	NA	-	-
DEBa_AF1	DE	Odernheim-am-Glan	AF	Or	SP	C	0.6-0.8	Dec-20	20	6	9
DEBa_AF2	DE	Odernheim-am-Glan	AF	Or	SP	C	0.6-0.8	Jun-21	20	6	9
DEBa_F1	DE	Odernheim-am-Glan	F	-	-	-	-	-	50	-	-
DEBa_F2	DE	Odernheim-am-Glan	F	-	-	-	-	-	50	-	-
DEBa_O1	DE	Odernheim-am-Glan	O	C	-	-	-	-	30	2,5	6
DEBa_O2	DE	Odernheim-am-Glan	O	C	-	-	-	-	30	1,5	3,5
ENWa_A1	EN	Metfield Lane	A	Or	-	-	-	-	NA	-	-
ENWa_A2	EN	Metfield Lane	A	C	-	-	-	-	NA	-	-
ENWa_AF1	EN	Metfield Lane	AF	Or	SA	-	-	-	24	1,30	8,5
ENWa_AF2	EN	Metfield Lane	AF	Or	SA	-	-	-	24	1,65	8,5
ENWa_AF3	EN	Metfield Lane	AF	Or	SA	-	-	-	24	7	7,5
ENWa_AF4	EN	Metfield Lane	AF	Or	SA	-	-	-	20	15	16
ENWa_F1	EN	Metfield Lane	F	-	-	-	-	-	20	-	-
ENWa_F2	EN	Metfield Lane	F	-	-	-	-	-	20	-	-
FLa_A1	FR	Saint-Genès-Champanelle	A	Or	-	S	2.25	Oct-20	NA	-	-
FLa_A2	FR	Saint-Genès-Champanelle	A	Or	-	S	2.25	Oct-20	NA	-	-
FLa_A3	FR	Saint-Genès-Champanelle	A	Or	-	S	2.25	Oct-20	NA	-	-
FLa_AF1	FR	Saint-Genès-Champanelle	AF	Or	SP	S	2.25	Oct-20	35	10	7
FLa_AF2	FR	Saint-Genès-Champanelle	AF	Or	SP	S	2.25	Oct-20	35	15	9
FLa_AF3	FR	Saint-Genès-Champanelle	AF	Or	SP	S	2.25	Oct-20	35	7	9
FLa_F1	FR	Saint-Genès-Champanelle	F	-	-	-	-	-	30	-	-
FLa_F2	FR	Saint-Genès-Champanelle	F	-	-	-	-	-	30	-	-
FLa_F3	FR	Saint-Genès-Champanelle	F	-	-	-	-	-	30	-	-
FRe_A1	FR	Prades-le-Lez	A	Or	-	-	-	-	NA	-	-
FRe_A2	FR	Prades-le-Lez	A	Or	-	-	-	-	NA	-	-
FRe_AF1	FR	Prades-le-Lez	AF	Or	SA	-	-	-	27	8	13
FRe_AF2	FR	Prades-le-Lez	AF	Or	SA	-	-	-	26	6	15
FRe_F1	FR	Prades-le-Lez	F	-	-	-	-	-	65	-	-
FRe_F2	FR	Prades-le-Lez	F	-	-	-	-	-	65	-	-
FRe_O1	FR	Prades-le-Lez	O	Or	-	-	-	-	27	7	7
FRe_O2	FR	Prades-le-Lez	O	Or	-	-	-	-	26	3	4

Field_ID	Country	Location	Habitat type	Management (Or=Organic; C=Conventional)	Agroforestry system (SA=silvo-arable- SP=silvo-pastoral)	Livestock used (C=cattle-S=sheep)	Stocking density (Large livestock units-ha)	Last grazing date	Tree age	Intra-row distance	Alley-width
IRELo_A1	IRE	Loughgall	A	Or	-	S	12	Oct-21	-	-	-
IRELo_A2	IRE	Loughgall	A	Or	-	S	12	Oct-21	-	-	-
IRELo_A3	IRE	Loughgall	A	Or	-	S	12	Oct-21	-	-	-
IRELo_AF1	IRE	Loughgall	AF	Or	SP	S	12	Oct-21	33	10	10
IRELo_AF2	IRE	Loughgall	AF	Or	SP	S	12	Oct-21	33	10	10
IRELo_AF3	IRE	Loughgall	AF	Or	SP	S	12	Oct-21	33	10	10
IRELo_AF4	IRE	Loughgall	AF	Or	SP	S	12	Oct-21	33	10	10
IRELo_F1	IRE	Loughgall	F	-	-	-	-	-	33	-	-
IRELo_F2	IRE	Loughgall	F	-	-	-	-	-	33	-	-
IRELo_F3	IRE	Loughgall	F	-	-	-	-	-	33	-	-
ITe_A1	IT	Paganico	A	Or	-	C	15	Jul-22	NA	-	-
ITe_A2	IT	Paganico	A	Or	-	C	15	Jul-22	NA	-	-
ITe_AF1	IT	Paganico	AF	Or	SP	C	15	Jul-22	90	-	-
ITe_AF2	IT	Paganico	AF	Or	SP	C	15	Jul-22	90	-	-
ITe_F1	IT	Paganico	F	-	-	-	-	-	75	-	-
ITe_F2	IT	Paganico	F	-	-	-	-	-	75	-	-
SDe_A1	SP	Plasencia	A	Or	-	C	0.3	Jul-22	-	-	-
SDe_A2	SP	Plasencia	A	Or	-	C	0.3	Mar-22	-	-	-
SDe_A3	SP	Plasencia	A	Or	-	C	0.6	Jul-22	-	-	-
SDe_AF1	SP	Plasencia	AF	Or	SP	C	0.3	Jun-22	175	-	-
SDe_AF2	SP	Plasencia	AF	Or	SP	C	0.3	Jul-22	175	-	-
SDe_AF3	SP	Plasencia	AF	Or	SP	C	0.6	Jul-22	175	-	-
SDe_F1	SP	Plasencia	F	-	-	-	-	-	10	-	-
SDe_F2	SP	Plasencia	F	-	-	-	-	-	10	-	-
SDe_F3	SP	Plasencia	F	-	-	-	-	-	20	-	-
SWMo_A	SW	Möhlin	A	C	-	-	-	-	-	-	-
SWMo_AF	SW	Möhlin	AF	Or	SA	-	-	-	15	10	23
SWMo_F	SW	Möhlin	F	-	-	-	-	-	15	-	-
SWMo_O	SW	Möhlin	O	C	-	-	-	-	15	4.5	7
SWSu_A	SW	Sursee	A	C	-	-	-	-	15	-	-
SWSu_AF	SW	Sursee	AF	C	SA	-	-	-	12	6	15
SWSu_F	SW	Sursee	F	-	-	-	-	-	15	-	-
SWSu_O	SW	Sursee	O	C	-	-	-	-	NA	0,8	4

Field_ID	Crop	Tree species	Tree density (nb trees/ha)	Tree (canopy) cover (%)	Bare soil (%)	Field size (ha)	Number of traps	Spider species richness	Simpson 1-D
DEBa_A1	-	-	-	0	5	7.09	12	33	0.8682
DEBa_A2	-	-	-	0	2	3.73	12	25	0.7354
DEBa_AF1	-	<i>Malus domestica</i>	110	45	5	1.65	12	30	0.8972
DEBa_AF2	-	<i>Malus domestica</i>	110	45	5	1.13	12	29	0.8042
DEBa_F1	-	Mixed broad leave tree stand (dominated by <i>Fagus sylvatica</i> and <i>Quercus sp.</i>)	NA	70	95	74.00	12	18	0.8561
DEBa_F2	-		NA	65	95	74.00	12	11	0.8255
DEBa_O1	-	<i>Malus domestica</i>	NA	10	0	0.46	12	25	0.8461
DEBa_O2	-	<i>Malus domestica</i>	NA	30	70	0.74	12	28	0.8779
ENWa_A1	permanent grassland	-	-	0	0	1.15	12	26	0.7317
ENWa_A2	winter wheat	-	-	0	100	42.72	11	12	0.7799
ENWa_AF1	herbal ley	<i>Corylus avellana</i>	1023	25	22.5	2.20	12	19	0.8567
ENWa_AF2	winter wheat	<i>Salix viminalis</i>	1269	20	21.25	2.98	11	16	0.8425
ENWa_AF3	herbal ley	Mixed tree stand	75	22.5	13.75	2.78	12	21	0.8314
ENWa_AF4	fallow	Walnut and plum trees	30	10	0	2.03	12	22	0.8609
ENWa_F1	-	Mixed broad leave tree stand (dominated by <i>Populus nigra x deltoides</i>)	400	38	0	0.97	11	14	0.5846
ENWa_F2	-		400	44.25	0	0.46	12	13	0.8188
FLa_A1	-	-	-	0	4	1.36	12	26	0.8291
FLa_A2	-	-	-	0	2.5	0.80	12	38	0.8223
FLa_A3	-	-	-	0	0	2.96	12	21	0.7951
FLa_AF1	-	<i>Fraxinus excelsior</i>	140	22.5	1.25	1.01	12	33	0.9352
FLa_AF2	-	<i>Acer pseudoplatanus</i> <i>Prunus avium</i>	60	31.25	0	0.81	12	30	0.8867
FLa_AF3	-	<i>Prunus avium</i>	150	47.5	0	0.90	12	26	0.9042
FLa_F1	-	Mixed broad leave tree stand (dominated by <i>Fraxinus excelsior</i> , <i>Prunus avium</i> and <i>Quercus sp.</i>)	NA	65	27.5	5.46	12	27	0.4254
FLa_F2	-		NA	65	15	2.79	11	18	0.1529
FLa_F3	-		NA	65	2.5	2.05	12	24	0.4339
FRe_A1	winter soft wheat	-	-	0	37.5	1.47	12	28	0.917
FRe_A2	vineyard	-	-	0	86	4.43	12	24	0.7788
FRe_AF1	winter soft wheat	<i>Juglans nigra x regia.</i>	96	75	53.75	3.86	12	23	0.916
FRe_AF2	vineyard	<i>Pinus pinea</i>	110	50	92.75	0.43	12	22	0.8732
FRe_F1	-	Garrigue tree stand (dominated by <i>Pinus sp.</i> and <i>Quercus ilex</i>)	NA	16.25	22.5	0.34	12	16	0.8537
FRe_F2	-		NA	17.5	25.5	3.56	12	18	0.9208
FRe_O1	-	<i>Juglans nigra x regia.</i>	204	41.25	12.5	1.47	12	25	0.8894
FRe_O2	-	<i>Pinus pinea</i>	1110	65	52.5	0.50	12	25	0.9398

Field_ID	Crop	Tree species	Tree density (nb trees-ha)	Tree (canopy) cover (%)	Bare soil (%)	Field size (ha)	Number of traps	Spider species richness	Simpson 1-D
IRELo_A1	-	-	-	0	0	0.38	8	13	0.7511
IRELo_A2	-	-	-	0	6.25	0.23	12	23	0.8413
IRELo_A3	-	-	-	0	3.75	0.34	11	13	0.761
IRELo_AF1	-	<i>Fraxinus excelsior</i>	200	77.5	10	0.62	12	23	0.8487
IRELo_AF2	-	<i>Fraxinus excelsior</i>	200	70	21.25	0.56	12	14	0.8506
IRELo_AF3	-	<i>Fraxinus excelsior</i>	200	56.25	10	0.54	12	22	0.8943
IRELo_AF4	-	<i>Fraxinus excelsior</i>	200	NA	0	1.44	11	20	0.7297
IRELo_F1	-	<i>Fraxinus excelsior</i>	1100	17.5	7.5	0.12	12	15	0.716
IRELo_F2	-	<i>Fraxinus excelsior</i>	1100	18.75	15	0.23	12	17	0.8547
IRELo_F3	-	<i>Fraxinus excelsior</i>	1100	76.25	5	0.16	12	15	0.7009
ITe_A1	-	-	-	0	0	2.50	11	13	0.8743
ITe_A2	-	-	-	0	13.5	3.70	12	10	0.8512
ITe_AF1	-	<i>Quercus cerris</i>	450	66.25	21.25	1.80	12	21	0.8026
ITe_AF2	-	<i>Quercus cerris</i>	450	76.25	71.75	7.50	10	8	0.4273
ITe_F1	-	<i>Quercus cerris</i>	600	28.75	80	6.40	9	17	0.8249
ITe_F2	-	<i>Quercus cerris</i>	600	35	83	6.40	6	6	0.3195
SDe_A1	-	-	-	0	13.75	15.64	12	15	0.7679
SDe_A2	-	-	-	0	0	14.47	11	14	0.8581
SDe_A3	-	-	-	0	20	21.08	12	10	0.8476
SDe_AF1	-	<i>Quercus ilex</i>	23,79	48.75	22.5	27.40	12	16	0.8583
SDe_AF2	-	<i>Quercus ilex</i>	12,53	25	6.25	65.37	12	21	0.923
SDe_AF3	-	<i>Quercus ilex</i>	4,19	55	13.75	20.80	12	14	0.9141
SDe_F1	-	<i>Quercus ilex</i> and <i>Quercus suber</i>	9,64	28.75	84	45.30	12	15	0.8391
SDe_F2	-		13,92	55	15	41.87	10	9	0.7365
SDe_F3	-		22,55	8.75	7.5	15.52	12	9	0.8595
SWMo_A	carrots and pastinak	-	-	0	31.5	2.50	12	12	0.758
SWMo_AF	peas and carrots	<i>Prunus avium</i> and <i>Sorbus torminalis</i>	70	22.5	19.25	0.06	12	17	0.8565
SWMo_F	-	Mixed tree stand (broad leave species)	NA	80	37.5	60.00	12	10	0.6279
SWMo_O	-	<i>Prunus avium</i>	352	8.75	4.25	1.56	12	26	0.4644
SWSu_A	strawberries	-	-	0	38.25	4.43	12	13	0.7492
SWSu_AF	strawberries	<i>Malus domestica</i>	105	25	50	5.75	12	20	0.8878
SWSu_F	-	Mixed tree stand (broad leave species)	NA	88.75	61.25	83.00	12	7	0.735
SWSu_O	-	<i>Malus domestica</i>	1500	8.75	18.25	0.46	12	14	0.6222



CHAPTER IV Figure S2 Mean spider abundance per habitat type

Significance levels: Significance levels: * $p < 0.05$, $0.001 < **p < 0.01$

CHAPTER IV Table S3 Results of linear mixed effects models showing total spider abundances differences between habitats calculated by post-hoc pairwise comparisons using the emmeans function (R package emmeans (Lenth, 2022)).

The table shows parameter estimates on the scale of the linear predictor. P-values < 0.05 are depicted in bold. Sampled habitat types are silvoarable systems, silvopastures, forests, orchards, croplands and pastures.

Habitat	Estimate	SE	df	t	P
Intercept	164.160	41.840	28.540	3.920	0.001
Silvoarable-silvopastoral	54.340	49.600	57.500	1.096	0.881
Silvoarable-Forest	69.370	42.000	60.000	1.651	0.569
Silvoarable-Orchard	-7.650	49.300	57.100	-0.155	1.000
Silvoarable-Cropland	13.820	45.300	53.500	0.305	1.000
Silvoarable-Pasture	-2.150	49.900	57.800	-0.043	1.000
Silvopastoral-Forest	15.030	31.100	57.000	0.484	0.997
Silvopastoral-Orchard	-61.990	48.200	59.900	-1.285	0.792
Silvopastoral-Cropland	-40.520	51.800	59.000	-0.782	0.970
Silvopastoral-Pasture	-56.480	32.100	53.100	-1.760	0.499
Forest-Orchard	-77.020	42.800	57.700	-1.799	0.474
Forest-Cropland	-55.550	44.700	59.800	-1.242	0.814
Forest-Pasture	-71.520	31.600	56.800	-2.262	0.227
Orchard-Cropland	21.470	50.600	55.700	0.424	0.998
Orchard-Pasture	5.500	48.500	59.900	0.113	1.000
Cropland-Pasture	-15.970	52.100	59.200	-0.306	1.000

CHAPTER IV Table S4 a) and b) Results of linear mixed effects models showing total species richness

(a) and Inverse Simpson index (b) differences between habitats calculated by

post-hoc pairwise comparisons using the emmeans function (R package emmeans (Lenth, 2022)).

The table shows parameter estimates on the scale of the linear predictor. P-values < 0.05 are depicted in bold.

Sampled habitat types are silvoarable systems, silvopastures, forests, orchards, croplands and pastures.

a)

SPECIES RICHNESS					
Habitat	Estimate	SE	df	t	P
Intercept	20.908	2.658	21.281	7.867	<0.001 ***
Silvoarable-silvopastoral	-0.544	2.750	60.000	-0.198	1.000
Silvoarable-Forest	6.364	2.310	58.900	2.756	0.080
Silvoarable-Orchard	-1.730	2.660	55.400	-0.649	0.987
Silvoarable-Cropland	0.901	2.440	53.200	0.369	0.999
Silvoarable-Pasture	1.963	2.770	59.900	0.709	0.980
Silvopastoral-Forest	6.909	1.680	55.600	4.100	0.002 **
Silvopastoral-Orchard	-1.186	2.640	58.300	-0.449	0.998
Silvopastoral-Cropland	1.445	2.870	59.700	0.504	0.996
Silvopastoral-Pasture	2.507	1.730	53.000	1.453	0.695
Forest-Orchard	-8.094	2.320	56.000	-3.488	0.012 *
Forest-Cropland	-5.464	2.450	58.100	-2.231	0.240
Forest-Pasture	-4.401	1.710	55.500	-2.568	0.123
Orchard-Cropland	2.631	2.730	54.600	0.963	0.928
Orchard-Pasture	3.693	2.650	58.200	1.391	0.732
Cropland-Pasture	1.062	2.880	59.700	0.369	0.999

b)

INVERSE SMPSON INDICES					
Habitat	Estimate	SE	df	t	P
Intercept	0.85573	0.05796	31.20884	14.765	<0.001 ***
Silvoarable-silvopastoral	0.0141	0.0741	48.5	0.19	1
Silvoarable-Forest	0.1657	0.064	58.3	2.588	0.1166
Silvoarable-Orchard	0.1123	0.0772	59	1.453	0.6945
Silvoarable-Cropland	0.0843	0.0718	53.9	1.174	0.8471
Silvoarable-Pasture	0.0317	0.0746	49.2	0.425	0.9981
Silvopastoral-Forest	0.1517	0.0485	58	3.125	0.0316 *
Silvopastoral-Orchard	0.0982	0.0741	59.2	1.325	0.7699
Silvopastoral-Cropland	0.0702	0.078	53.4	0.9	0.9449
Silvopastoral-Pasture	0.0176	0.0508	53.2	0.347	0.9993
Forest-Orchard	-0.0535	0.0669	59.3	-0.8	0.9665
Forest-Cropland	-0.0815	0.0686	59.8	-1.187	0.8414
Forest-Pasture	-0.134	0.0494	57.8	-2.713	0.0881
Orchard-Cropland	-0.028	0.0796	57.1	-0.352	0.9993
Orchard-Pasture	-0.0806	0.0745	59.4	-1.081	0.887
Cropland-Pasture	-0.0526	0.0785	53.9	-0.67	0.9845

STATUS AND AUTHOR CONTRIBUTIONS OF PUBLICATIONS

CHAPTER II

Edo M, Entling MH, Rösch V (2024) Agroforestry supports high bird diversity in European farmland. *Agron Sustain Dev* 44:1–12 <https://doi.org/10.1007/s13593-023-00936-2>

Agronomy for Sustainable Development, published online 20th December 2023

All authors contributed to the study conception and design. Material preparation, data collection, and analysis were performed by Manon Edo. 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

CHAPTER III

Edo M, Entling MH, Herzog F, Noe K, Palma JHN, Seithe A, Rösch V (2025) Agroforestry systems favor bat conservation but only when old and grazed. *Glob Ecol Conserv* 57:e03369 <https://doi.org/10.1016/j.gecco.2024.e03369>

Global Ecology and Conservation, published online 17th December 2024

Manon Edo, Martin H Entling, Felix Herzog, João HN Palma, Will Simonson, Jo Smith and Verena Rösch contributed to the study conception and design. Manon Edo, Anja Weiler, João HN Palma, Will Simonson and Jo Smith collected the data. Manon Edo, Verena Rösch, Kira Noe, Ayla Seithe and Anja Weiler analyzed the data. Manon Edo led the writing, and Manon Edo, Martin H Entling, Felix Herzog, João HN Palma, Will Simonson, Jo Smith and Verena Rösch contributed to the finalization of the manuscript. All authors read and approved the final version of the manuscript.

CHAPTER IV

Edo M, Herzog F, Moreno M, Olave R, Ripamonti A, Rösch V, Simonson W, Tramacere LG, Villepoux O, Entling MH (2025) The potential of agroforestry and small fields to enhance ground-dwelling spiders.

Submitted to Agroforestry Systems

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ILLUSTRATIONS

All illustrations in this work were drawn by Manon Edo.

DECLARATION OF GENERATIVE AI TECHNOLOGIES IN THE WRITING PROCESS

During the revision of the abstract, general introduction, and the synthesis and outlook chapters, the author made selective use of DeepL and ChatGPT-4 to improve grammar, spelling, and phrasing in English. All content generated with these tools was carefully reviewed and edited by the author, who takes full responsibility for the final version of the text.



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ACADEMIC PUBLICATIONS

Edo, M., Villepoux, O., Rösch, V., Tramacere, L. G., Ripamonti, A., Simonson, W., Moreno, G., Herzog, F., Olave, R., & Entling, M. (to be submitted). The potential of agroforestry and small fields to enhance ground dwelling spiders. Submitted to *Agroforestry Systems*.

Edo, M., Entling, M. H., Herzog, F., Noe, K., Palma, J. H., Seithe, A., Simonson, W., Smith, J., Weiler, A., & Rösch, V. (2025). Agroforestry systems favor bat conservation but only when old and grazed. *Global Ecology and Conservation*, 57, e03369. <https://doi.org/10.1016/j.gecco.2024.e03369>

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Stahl, L. F., **Edo, M.**, Nonnenmacher, T., Reif, D., Rex, F., Wegmann-Herr, P., Kortekamp, A., Fischer-Schuch, J., Thines, E., & Scharfenberger-Schmeer, M. (2022). Ozonized oleic acid as a new viticultural treatment? Study of the effect of LIQUENSO® Oxygenate on the carpoplane microbial community and wine microorganisms combining metabarcoding and in vitro assays. *Ecologies*, 3(3), 292–307. <https://doi.org/10.3390/ecologies3030023>

CONFERENCE CONTRIBUTIONS

Edo, M., Entling, M.H., Rösch, V. (2024). Agroforestry to support spider diversity in Europe. Oral presentation at the 34th European Congress of Arachnology (ECA), 26–30 August 2024.

Edo, M., Entling, M.H., Rösch, V. (2024). Agroforestry to support bat conservation in Europe. Oral presentation at the 7th European Agroforestry Conference (EURAF), 27–31 May 2024.

Edo, M., Entling, M.H., Rösch, V. (2023). Systèmes agroforestiers en Europe: un habitat pour les chiroptères ? Etude des communautés et de l'activité des chiroptères dans des systèmes agrisylvicoles et sylvopastoraux. Oral presentation at the Rencontres chiroptères Alsace, 29-31 Septembre 2023.

Edo, M., Entling, M.H., Rösch, V. (2022). Breeding birds in European agroforestry systems. Oral presentation at the 6th European Congress of Conservation Biology (ECCB), 22-26 August 2022.

Edo, M., Entling, M.H., Rösch, V. (2022). Breeding birds in European agroforestry systems. Oral presentation at the 6th European Agroforestry Conference (EURAF), 16-20 May 2022.

OTHER ORAL PRESENTATIONS AND PUBLICATIONS

Edo, M., Entling, M.H., Rösch, V. (2025). Vergleich der Biodiversität von Agroforst-Systeme mit und ohne Beweidung. Oral presentation at Pollichia Tagung, 15 March 2025.

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DECLARATION

I hereby declare that I independently conducted the work presented in this thesis entitled Effects of Agroforestry in Birds, Bats and Spiders in Europe. All used assistances are mentioned and involved contributors are either co-authors of or are acknowledged in the respective publication. This thesis has never been submitted elsewhere for an examination, as a thesis or for evaluation in a similar context to any department of this university or any scientific institution. I am aware that a violation of the aforementioned conditions can have legal consequences.

Manon Edo, Landau, 16.05.2025