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Evaluating the effects of agroforestry versus arable systems on functional biodiversity and associated ecosystem services

Doctor of Philosophy Thesis

Sustainable Land Management

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Declaration

I confirm that this is my own work and the use of all material from other sources has been properly and fully acknowledged.

Tom Staton

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Abstract

The intensification of agricultural production in recent decades is widely recognised to have contributed substantially to global declines in biodiversity and associated ecosystem services, such as natural pest control and pollination. Agroforestry systems, where trees and/or shrubs are integrated into agricultural fields or landscapes, have the potential to increase biodiversity and associated ecosystem services. This thesis therefore aims to evaluate how agroforestry systems affect invertebrate pests, their natural enemies, and pollinators, in addition to productivity and farm income, relative to arable monocultures. A review and meta-analysis of the literature revealed that arthropod pests are significantly suppressed, and natural enemies significantly enhanced, in agroforestry systems relative to arable monocultures. However, the results were equivocal with high heterogeneity. Empirical data collected from three agroforestry sites with paired arable controls confirmed higher levels of plant and invertebrate biodiversity in agroforestry systems, and also revealed that the agroforestry systems led to a change in plant and invertebrate communities. These changes could be explained in terms of life-history traits, for example, plant communities in agroforestry systems were more perennial while invertebrates were less likely to be winged. Functional trait diversity of natural enemies was significantly higher in the agroforestry systems, indicating a higher level of biological control. Furthermore, species-level pollinator data from the same sites revealed that additional bee species in agroforestry contributed to functional trait diversity through niche complementarity. To further explore causes of heterogeneity, understorey management was manipulated at one agroforestry site, and was found to significantly affect natural enemy abundance and diversity, aphid suppression, and pollinator visitation. Although arable yields were up to 11% lower in agroforestry than arable systems, financial modelling predicted that agroforestry systems were capable of increasing farm income after at least seven years. Agroforestry systems therefore represent a viable option to restore farmland biodiversity and improve agricultural sustainability.

Contents

1. Introduction

1.1 Agricultural sustainability

The intensification of agricultural production systems in the UK and globally over recent decades has resulted in substantial changes in land use and management, such as increased field sizes, decreased spatial and temporal crop diversity, removal of hedgerows and other non-cropped habitats, deep ploughing, and increased use of synthetic fertilisers and plant protection products (Garibaldi et al. 2017; Tscharntke et al. 2005). This is widely acknowledged to have contributed substantially to declines in biodiversity and associated ecosystem services (Bartomeus et al. 2014; Rusch et al. 2016; Tscharntke et al. 2005).

Strategies to improve the sustainability of agricultural production include sustainable intensification, ecological intensification, and diversified farming systems (Box 1), which are compatible concepts. All of these strategies share the common goal of improving food security and protecting nature-based ecosystem functions and services on which sustainable food production depends (FAO 2013; Garibaldi et al. 2017), therefore reducing dependency on unsustainable and environmentally damaging inputs (Bommarco et al. 2013). At the farm level, forms of sustainable agricultural management include strategies to reduce pesticide inputs such as Integrated Pest Management (IPM) or organic systems, soil conservation strategies such as conservation tillage and cover cropping, and diversified farming such as intercropping, agroforestry systems, and the provision of non-cropped habitats such as field margins, flower strips, beetle banks, or hedgerows (e.g. Garibaldi et al. 2014; Gontijo 2019). However, these more sustainable approaches to food production have seen limited uptake globally, in part because of a lack of evidence as to the risks, costs and benefits of these approaches compared with ‘business as usual’ farming, at the farm-scale and across the full crop rotation (Chaplin-Kramer et al. 2019; Kleijn et al. 2019).

Box 1: Sustainable approaches to agricultural production

Sustainable intensification (SI) aims to increase overall agricultural production through higher global yields, while also improving food security through environmental sustainability, such as reducing inputs and minimising use of additional land for agriculture (Petersen & Snapp 2015; Pretty 1997). SI is context-specific, such that in some locations yield reductions may be required to improve sustainability (Garnett et al. 2013).

Ecological intensification is a more specific, process-based framework which seeks to harness ecological processes, including natural pest control and pollination, to improve agricultural production (Bommarco et al. 2013; Tittonell 2014).

Diversified farming systems reflect a suite of farming practices that intentionally integrate functional biodiversity to maintain ecosystem services, thereby relying on internal regeneration rather than external inputs (Kremen et al. 2012). The priority given to ecological processes mean that crop yields can be lower than non-diversified systems, at least in the short-term (Rosa-Schleich et al. 2019).

1.2 Introducing agroforestry as a sustainable farming system

Agroforestry systems, which are essentially ‘farming with trees’ (Gordon et al. 2018), have been proposed as a ‘win-win’ for environmental protection and crop production (International Assessment of Agricultural Knowledge Science and Technology for Development 2009; The Woodland Trust 2018). A number of definitions of agroforestry have been put forward over the past few decades, which typically emphasise the intentional integration of trees, and the economic, environmental and productivity benefits arising from interactions between the agricultural and tree components, for example:

> “*the purposeful growing or deliberate retention of trees with crops and/or animals in interacting combinations for multiple products or benefits from the same management unit*” (Nair 1993)

> "*Intensive land-use management that optimizes the benefits (physical, biological, economic, social) from biophysical interactions created when trees and/or shrubs are deliberately combined with crops and/or livestock.*" (Gold & Garrett 2009)

Agroforestry is therefore a broad definition in terms of its scale, composition, and configuration. For example, at the landscape scale, agroforestry systems include hedgerow networks or shelterbelts bounding agricultural fields, while field-scale agroforestry systems include wood pasture, undergrazed orchards, and trees intercropped with arable. Agroforestry systems have been categorised into six broad types in Europe, comprising silvoarable, forest farming, riparian buffers, silvopasture, improved fallow, and multipurpose trees (Mosquera-Losada et al. 2009). In the EU, agroforestry systems are estimated to cover 3.6% of land area, or 8.8% of agricultural land, over 90% of which comprises silvopasture (livestock agroforestry systems), with the majority located towards the south of the continent (den Herder et al. 2017). Globally, agroforestry systems are more prominent in tropical regions because of differing labour and machinery requirements (Zomer et al. 2016).

This thesis specifically focusses on silvoarable agroforestry systems in the UK, although many of the conclusions are relevant to temperate regions or even globally. Silvoarable systems, also known as agrisilviculture (MacDicken & Vergara 1990), is essentially trees on arable land, and in Europe has been defined as "widely spaced trees inter-cropped with annual or perennial crops" (Mosquera-Losada et al. 2009). There is a particular need to restore biodiversity and associated ecosystem services on arable land, given the potential economic impacts of pest damage and pollination deficits, as discussed in the sections below. Hence, silvoarable systems offer an opportunity to improve the sustainability of food production, but currently comprise a small proportion of agroforestry in Europe (den Herder et al. 2017) and have potential for larger-scale implementation if sufficient evidence can be provided and communicated.

In temperate regions, silvoarable systems typically comprise rows of trees and/or shrubs separated by crop alleys, in a configuration termed alley cropping. The rows of woody vegetation most commonly comprise a single line of trees/shrubs over a 2 to 3 m wide uncultivated strip which may be seeded with a cover crop, a flower mix, or maintained as bare ground (Reubens 2018). Arable crop alleys are typically between 12 and 24 m in width to allow sufficient access for modern farm machinery for management operations such as cultivation, harvest, and agrochemical application. Silvoarable systems in Europe typically utilise fruit trees, fast-growing timber trees, short-rotation coppice (Fig. 1.1) or, in the south of the continent, olives and oaks (Eichhorn et al. 2006).

Figure 1.1. Examples of silvoarable systems in northern Europe. Clockwise from top-left: apple-based system, poplar timber system, mixed apple and timber, short-rotation coppice system. Photo credits: Thomas Lecomte, Paul Burgess, Jo Smith (bottom two).

Agroforestry systems have a long history, and traditional forms of agroforestry can be seen throughout the world, for example wood pastures, hedgerows, and grazed orchards in Europe (Smith 2010), and the deliberate retention or planting of trees to provide shelter for crops in the tropics (Nair 1993). More recent agroforestry systems have since been developed to be compatible with modern farming practices, such as large machinery (Smith et al. 2012).

Research has demonstrated that agroforestry systems can provide a range of environmental and productivity benefits in temperate regions. For example, a meta-analysis found significant positive effects of agroforestry systems in Europe on erosion control, biodiversity, and soil fertility compared with monoculture agriculture and forestry, although biomass production was lower in agroforestry systems (Torralba et al. 2016). The positive effects on biodiversity were however only significant for silvopasture systems, and not for silvoarable systems. The strongest positive biodiversity effects of agroforestry systems were on birds, while the effects on plants, fungi and insects were weaker and non-significant. Previous review articles have identified the potential for agroforestry systems to provide other ecosystem service benefits including carbon sequestration, water quality, air quality and productivity (Smith et al. 2013a; Tsonkova et al. 2012). In addition, Stamps and Linit (1998) identified the potential for temperate agroforestry systems to enhance natural pest control, although this was largely based on theoretical potential with limited evidence available at the time.

The purported environmental benefits, such as biodiversity and landscape aesthetics, are seen as the main positive aspects of agroforestry systems amongst farmers and stakeholders in Europe, while management, socio-economic constraints and a lack of knowledge and awareness have been identified as the main barriers to adoption (García de Jalón et al. 2018; Graves et al. 2017; Rois-Díaz et al. 2018). A survey of UK farm owners found that although biodiversity was the second most frequently mentioned benefit of agroforestry systems, the attraction of mammal or insect pests was frequently identified as a negative aspect (Lewis 2011). As such, there is a research need to better understand the trade-offs of biodiversity in agroforestry systems, i.e. the extent to which the recognised biodiversity benefits of agroforestry systems translate into ecosystem functions and services, such as pollination and the control of pests via natural enemies, versus ecosystem disservices such as crop damage by pests (Fig. 1.2).

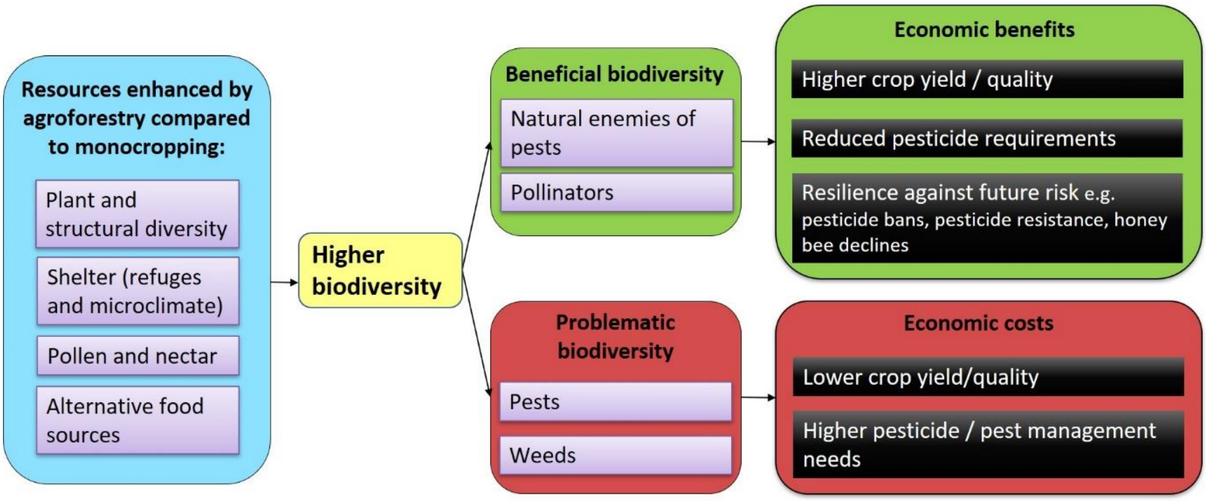

Figure 1.2. Flow diagram to summarise the benefits of agroforestry systems on biodiversity, which can then lead to benefits and ecosystem services such as natural pest control and pollination, or disservices in the form of pest or weed pressure.

1.3 Natural pest control

Global crop loss due to arthropod pests has been estimated at 18 to 26% (Culliney 2014). Therefore, effective methods to suppress pests and minimise subsequent crop damage are of high economic and social importance. In recent decades, agricultural production has become increasingly reliant on plant protection products such as pesticides, because of their ability to provide highly effective short-term control of pests. For example, global pesticide use is predicted to have increased 15-20 fold between 1960 and 2003 (Oerke 2006). The reliance of agricultural production on pesticides has been widely recognised as unsustainable, because of the emergence of pesticide resistance together with the loss of naturally occurring predators of pests (Hawkins et al. 2019; Mallet 1989), while there are concerns as to the environmental and human health impacts (Aktar et al. 2009; Alavanja et al. 2004; Pimentel 2005).

Furthermore, the depletion of invertebrate natural enemies (such as predators and parasitoids) of pests and other ecosystem changes caused by preventative pesticide application can lead to target pest resurgence, where the pest population rebounds to a higher density than an untreated control or pre-treatment density, or to secondary pest outbreaks, where previously unproblematic species emerge as pests (Dutcher 2007; Hardin et al. 1995). Once pesticides are adopted, there is a risk that farmers become ‘locked in’ to pesticide dependency because of the high initial cost of switching to more sustainable methods and the depletion of natural enemy populations (Bakker et al. 2020; Wilson & Tisdell 2001).

An alternative or complementary tactic for controlling pests is natural pest control, which seeks to suppress pests through plant diversification and associated disruption of resource concentration (‘bottom-up’ effects), and/or through ‘top-down’ predation or parasitism of pests by encouraging locally-occurring natural enemies through conservation biological control (Gurr et al. 2017). Although natural pest control is seen as more sustainable than chemical control because natural enemies co-evolve with their prey, measures to promote natural pest control are often associated with higher farm management complexity, a time-lag between implementation and any observable benefits, and a greater degree of uncertainty as to its efficacy compared with the ‘quick fix’ provided by pesticides (Kleijn et al. 2019; Straub et al. 2008; Tscharntke et al. 2016).

1.4 Pollination

An estimated 35% of global crop production is derived from crops dependent on pollinators, while 70 of 87 leading food crops are at least moderately dependent on pollinators (Klein et al. 2006). Pollen limitation inhibits yield growth and stability in pollinator-dependent crops (Garibaldi et al. 2011). Insects are the major pollinators in temperate regions, with bees typically recognised as the most important while other contributors include flies, butterflies and solitary wasps (Klein et al. 2006; Willmer et al. 2017). The decline of wild insect pollinators, largely driven by the intensification of agriculture and other land-uses, has led to a reliance on managed pollinators, such as honeybees *Apis mellifera*, to provide pollination services (Aizen & Harder 2009; Vanbergen et al. 2013).

The sustainability of reliance on a low number of managed species to provide a high proportion of pollination services is threatened by declines in colony numbers or growth deficits relative to the increasing demand for crop pollination in agriculture (Aizen & Harder 2009; Breeze et al. 2014; Potts et al. 2010; Smith et al. 2013b). Wild pollinators could play an important functional role in pollination services by contributing to productivity, quality, and yield stability of pollination-dependent crops through niche complementarity (Garibaldi et al. 2014; MacInnis & Forrest 2019; Vasiliev & Greenwood 2020), in addition to providing insurance against managed honey bee declines (Winfree et al. 2007).

1.5 Natural pest control and pollination: theoretical potential of agroforestry systems

1.5.1 Plant and habitat diversity

Increased diversification of crop and/or non-crop plants in agricultural systems has long been recognised as having the potential to improve natural pest control and pollination. For example, the resource concentration hypothesis predicts that dietary-specialist herbivorous invertebrates should be less abundant as plant diversity increases, because continuous patches of host plants are easier for specialist-diet herbivores to find, remain in and proliferate, compared with more botanically diverse patches (Root 1973). This can lead to significantly reduced herbivore load and/or crop damage in diversified systems relative to monocultures, although there is considerable variation in effects among different studies (Andow 1991; Letourneau et al. 2011; Tonhasca & Byrne 1994).

The enemies hypothesis complements the resource concentration hypothesis by predicting that natural enemies are more effective at controlling herbivores in complex environments due to a greater diversity of prey, hosts and microhabitats (Root 1973). Empirical evidence generally supports this hypothesis, although again there is substantial heterogeneity among responses (Andow 1991; Letourneau et al. 2011; Russell 1989). Natural enemy abundance can also benefit from structural complexity of habitats (Langellotto & Denno 2004), because the higher availability of refuges reduces intraguild predation (Finke & Denno 2006).

Plant diversity, particularly in terms of flower resources, has been demonstrated to increase pollinator functional diversity and pollination metrics, by increasing floral resource complementarity for different pollinator groups, and by increasing the temporal continuity of floral resources (Isbell et al. 2017; Nicholls & Altieri 2013; Sutter et al. 2017). A higher diversity of floral resources also improves the stability of pollination services, via spatio-temporal niche complementarity (Venjakob et al. 2016), while habitat diversity and especially the availability of untilled land can provide critical nesting resources (Kremen et al. 2007; Nicholls & Altieri 2013).

Silvoarable agroforestry systems are inherently more structurally, botanically and floristically diverse than monoculture arable systems. Although the extent of the increased diversity is dependent on system design and management, based on the above hypotheses, natural pest control and pollination are predicted to be enhanced in agroforestry compared with arable systems. Expectations for the effects of agroforestry systems on natural pest control and pollination can be further informed by more specific considerations of habitat features and resource requirements of functional groups.

1.5.2 Habitat features and mechanisms

Gurr et al (2017) identified four mechanisms through which habitat management can enhance the effectiveness of natural enemies of pests, denoted by the mnemonic ‘SNAP’: shelter, nectar, alternative prey or hosts, and pollen. These resources also provide nesting and foraging habitat for pollinators (Senapathi et al. 2015; Vasiliev & Greenwood 2020). However, negative effects (i.e. ecosystem disservices) can also potentially arise from these resources, for example if they benefit crop pests, increase intra-guild natural enemy predation or if non-crop flowers compete with crops for pollinators (Gurr et al. 2017). The potential for these mechanisms to alter the balance of ecosystem services and disservices in silvoarable systems, relative to arable systems, is briefly reviewed below.

Shelter

Shelter can refer to (i) perennial vegetation features which provide year-round habitat sources, particularly for over-wintering of natural enemies and nesting for pollinators, and (ii) microclimatic shelter effects such as windbreaks. Both mechanisms are relevant to the comparison between silvoarable and arable systems.

Arable management operations, such as tillage and pesticide application, can lead to direct mortality, indirect fitness effects and emigration of beneficial fauna such as pollinators and the natural enemies of pests (Desneux et al. 2007; Rowen et al. 2020; Thorbek & Bilde 2004). Therefore, refuges featuring low levels of disturbance, which is typically a feature of silvoarable tree rows, are important source habitats for natural enemies and pollinators, from which they can disperse into arable fields (Alignier et al. 2014; Lee et al. 2001; Öckinger & Smith 2007). These source habitats can provide favourable overwintering conditions compared with arable fields, for example natural enemies which overwinter in non-crop habitats respond most strongly to fine-grained landscapes with high edge densities (Gallé et al. 2018; Haan et al. 2020). As such, recent research has focussed on strategies such as beetle banks, hedgerows, and flower strips to enhance the effectiveness of natural enemies and pollinators in arable landscapes (Albrecht et al. 2020; Garratt et al. 2017; MacLeod et al. 2004; Morandin & Kremen 2013). Silvoarable tree rows could be seen as analogous to these features, while also directly contributing to productivity and farm income.

In terms of microclimate, agroforestry tree rows act as a windbreak, the extent of which depends on a number of factors including tree height, permeability and orientation (reviewed in Quinkenstein et al. 2009). Even tree rows of 3 to 5 m height significantly reduce windspeeds in adjacent crop alleys compared with open field conditions (Kanzler et al. 2019). In addition to improving flight conditions and foraging/hunting success for insect pollinators and aerial natural enemies such as parasitoids (Hennessy et al. 2021; Vosteen et al. 2020), the windbreak effect could disrupt dispersal by pests dependent on air currents, particularly wingless and small-sized insects (Pasek 1988).

Nectar and pollen

Depending on tree row management, silvoarable systems have the potential to increase the availability of nectar and pollen resources compared with monoculture arable systems. Nectar provides an important energy source for airborne insects including pollinators and some natural enemies. For example, the adult stages of parasitoids and aphidophagous hoverflies feed on nectar (Landis et al. 2000). Pollen provides a higher source of protein compared with nectar, which is critical for larval development in bees, and increases the longevity and fecundity of natural enemies such as hoverflies and parasitoids (reviewed in Lu et al. 2014).

Floral resources have been shown to be more important than aphid prey and grass habitats for the abundance of aphid natural enemies such as parasitoids, hoverflies and ladybirds (Ramsden et al. 2015). Furthermore, a pollinator model predicted that flower margins without nesting resources increased bumblebee populations to a greater extent than grassy margins offering nesting resources (Häussler et al. 2017). Many natural enemies, such as hoverflies, require a shallow flower depth to access the nectar, while extrafloral nectaries are important for parastioids (Landis et al. 2000; van Rijn & Wäckers 2016). By contrast, some pollinators have co-evolved long tongues with complex-structured flowers such as long corolla tubes that are inaccessible to short-tongued species (Fenster et al. 2004). Other relevant floral characteristics includes colour, flowering time and nectar chemistry (Gurr et al. 2017). Therefore, it is predicted that the functional diversity of flower types in a silvoarable system will influence the functional diversity of natural enemy and pollinator communities.

Finally, silvoarable systems offer a potential advantage over other strategies such as flower margins by providing a regular source of pollen and nectar throughout a field rather than being confined to field edges. This could encourage a higher spatial evenness of natural enemies and pollinators, particularly smaller species with limited dispersal capabilities such as parasitoids and small bees (Vollhardt et al. 2010). For example, positive effects of flower availability in field margins on natural enemies were only observed up to 5 m into an adjacent field (Mei et al. 2021). However, silvoarable systems could also confer a potential for ecosystem disservices by providing habitat which may promote higher pest abundances (e.g. Baggen et al. 1999).

Alternative hosts and prey

Temporal continuity of food sources is an important factor determining populations of natural enemies and pollinators, for example, many parasitoids require alternative hosts on non-crop species over winter (e.g. Landis et al. 2000; Murphy et al. 1998), while pollinators benefit from seasonal continuity of flower resources (Timberlake et al. 2019). Higher biodiversity can therefore help to sustain beneficial invertebrates by providing a higher diversity of food sources. For natural enemies, this can include alternative prey such as springtails (Collembola), which can benefit carabid beetle and spider populations in conservation tillage systems (Roger-Estrade et al. 2010; Tamburini et al. 2016). The availability of alternative prey can however be counter-productive if they distract natural enemies from predating crop pests (Symondson et al. 2006).

1.6 Productivity and farm income

Research into sustainable agricultural systems has traditionally focussed on the potential environmental benefits such as ecosystem services. There has recently been recognition of a mismatch between the aims of research and the interests of farmers, who are more motivated by objectives relating to productivity, profitability and financial risk at realistic temporal and spatial scales, i.e. across the rotation at the farm level (Chaplin-Kramer et al. 2019; Kleijn et al. 2019).

A key aim of agroforestry systems is to maintain or enhance productivity compared with monocultures, and this is reflected in some of the definitions of agroforestry (as explained above). In this respect, agroforestry systems differ from many other forms of ecological intensification which take land out of production, such as flower strips and non-production hedgerows. However, the level of productivity depends on complementary use of water, light and nutrient resources between the tree and annual crop (Cannell et al. 1996). The productivity of agroforestry systems in northern Europe is typically limited by light availability, whilst water availability is more limiting in southern Europe (McAdam et al. 2008). At higher latitudes, tree rows in silvoarable systems are usually planted in a north-south orientation, to minimise shading impacts on the crop. The availability of light and water affects the components of the system differently, i.e. crop growth is strongly limited by shade, whereas water availability primarily inhibits tree growth (Burgess et al. 2005).

A key constraint for the adoption of agroforestry systems is cash flow, i.e. the time delay associated with receiving a financial return relative to ‘business as usual’ farming (García de Jalón et al. 2018). The duration of this breakeven time depends on the choice of tree, for example, slower-growing timber trees such as walnut and cherry are expected to provide revenue 60 years after planting, whilst poplar provides a return after 20 years (Graves et al. 2007). Fruit trees such as apple have the potential to provide a more rapid return, and therefore this system is receiving increased interest amongst farmers in the UK in particular (Newman et al. 2018).

One way to overcome the cash-flow limitation of agroforestry systems is by providing grant support. For example, the establishment of agroforestry systems is included as an option in the European Union’s Common Agricultural Policy (Article 23 of Regulation 1305/2013), and various member states (but not England) activated this policy to provide an initial planting payment followed by annual maintenance payments. In addition, agroforestry is being considered for support in England’s emerging Environmental Land Management scheme (Rural Payments Agency 2021). Recent studies have sought to factor in the environmental benefits of agroforestry systems into cost-benefit analyses. These environmental benefits include carbon sequestration, reductions in greenhouse gas emissions, reductions in nitrogen and phosphorous surplus, soil retention and groundwater recharge. Agroforestry systems can become more profitable than ‘business as usual’ alternatives after factoring in the economic value of these externalities (García de Jalón et al. 2017; Kay et al. 2019a).

1.7 Research needs

The majority of research of functional biodiversity in agroforestry systems is based in the tropics. For example, a meta-analysis of the effect of agroforestry systems on pests and weeds included only two studies from temperate regions, compared with 40 from the tropics or sub-tropics (Pumariño et al. 2015). A review was published over 20 years ago relating to arthropod communities and natural pest control in temperate agroforestry systems (Stamps & Linit 1998), but further evidence has since emerged. Although previous studies have investigated certain aspects and taxonomic groups of biodiversity in temperate silvoarable systems, many of these are only available as unpublished reports, theses or paper-only conference abstracts (e.g. Burgess et al. 2003; Naeem et al. 1997; Rekany 2015).

Furthermore, there appears to be considerable inconsistency in the literature, for example, the abundance of natural enemies in temperate silvoarable compared with arable systems has variously been reported to be higher (e.g. Peng et al. 1993) or lower (e.g. Burgess et al. 2003). The same can be said for pest abundances (Griffiths et al. 1998; Stamps et al. 2002). As such, given that the existing evidence is fragmentary and apparently inconsistent, there is a need to synthesise the results of published and unpublished studies on pest, natural enemy and pollinator communities in temperate silvoarable systems, and to investigate the drivers of this heterogeneity.

Although the benefit of agroforestry systems to pollinator biodiversity appears to be more consistent, there is a lack of understanding as to the relationship between biodiversity and ecosystem functioning (e.g. pollination) in agricultural systems generally (Blüthgen & Klein 2011; Nicholson et al. 2020). By studying how additional species in agroforestry systems contribute to functional trait diversity, it is possible to reveal whether these species merely contribute to functional redundancy, or improve ecosystem functioning (Villéger et al. 2008; Woodcock et al. 2019).

A limitation of the current literature on invertebrate biodiversity in agroforestry systems is taxonomic breadth. As set out in Chapter 2, only two studies of pests and natural enemies in temperate silvoarable systems included more than four taxonomic orders, while species-level pollinator studies are limited to bees (Varah et al. 2020). This limits our understanding of why and to what extent different taxa vary in their response to farming system (agroforestry vs arable). Any such inter-taxon heterogeneity could potentially be explained mechanistically by studying their traits. Trait-based approaches are widely used in ecology, but their application to invertebrates in agro-ecosystems is more embryonic (Gagic et al. 2015; Wong et al. 2019). For example, the application of these approaches to functional biodiversity in temperate silvoarable systems is limited to a study on carabid beetles and weeds in France (Boinot et al. 2019a, b).

As our understanding of the advantages and disadvantages of agroforestry systems on pests, natural enemies and pollinators develops, another research need is to investigate how to maximise the eco-functionality of silvoarable systems through appropriate design and management. For example, there is currently a scarcity of evidence as to how the tree row understorey in a silvoarable system should be managed for biodiversity and production benefits. Various options have been implemented, such as regular mowing, maintenance of bare ground, or sowing a cover crop or flower mix (Reubens 2018). Although comparisons have been made between vegetated and bare understoreys on limited aspects of biodiversity (Burgess et al. 2003; Smits et al. 2012), the effects of management on functional biodiversity and ecosystem services are poorly understood in silvoarable systems.

Finally, the uptake of silvoarable systems by arable farmers will ultimately depend to a large degree on its economic performance compared with arable monocultures. In particular, the time taken to recuperate establishment costs is likely to be a critical factor, given that cashflow is viewed as a negative aspect of agroforestry systems (García de Jalón et al. 2018). Although the economics of timber silvoarable systems have been relatively well studied, fruit-based systems such as intercropping with apple trees have not, despite recent interest amongst farmers in the UK (Newman et al. 2018).

Based on the research needs identified above, the aim of this thesis is to evaluate how silvoarable agroforestry systems affect above-ground plant and invertebrate functional biodiversity, associated ecosystem services (natural pest control and pollination), and farm income, relative to arable monoculture systems. To address this aim, this thesis broadly has the following key objectives:

1. Review and analyse information from previous studies of biodiversity, and in particular invertebrate natural enemies, pests and pollinators, in temperate silvoarable systems to understand the current state of evidence and identify specific research needs;
2. Collect new plant and invertebrate community data to evaluate taxonomic and functional trait differences between silvoarable and monoculture arable systems at a broad taxonomic scale;
3. Investigate the influence of tree row understorey management on community composition of functional groups and associated ecosystem services;
4. Analyse the financial cost-benefits and sensitivity of silvoarable systems relative to equivalent arable systems.

1.8 Thesis structure

Chapter 2 relates to the first objective above. It comprises a review and meta-analysis of the literature, aiming to evaluate the current state of knowledge of pests, natural enemies, and pollinators in temperate silvoarable systems. In addition, the discussion of this chapter aims to develop a predictive framework to account for variation in effects among different studies, upon which hypotheses can be generated for future research.

Chapters 3 to 6 are data chapters. Using data collected from field sites, Chapter 3 aims to address the second objective above by comparing communities of plants, invertebrate pests and their natural enemies, between silvoarable and arable systems, using both taxonomic and functional trait approaches.

Chapter 4 further explores the second objective above, in the context of pollinators, by comparing functional diversity of bees and hoverflies in silvoarable versus arable systems. This chapter aims to advance our understanding of the biodiversity-ecosystem functioning relationship in agroforestry systems, by using species-level data to investigate functional identity and functional diversity metrics, and the role of rarer species.

Chapter 5 aims to address the third objective above, by investigating the effect of understorey management in a silvoarable system on functional invertebrate biodiversity and associated ecosystem services in both the tree and arable crop components.

Chapter 6 evaluates agricultural productivity, farm income and the contribution of biodiversity in silvoarable versus arable systems, using a combination of ecosystem service and financial cost-benefit models. This chapter integrates findings from Chapter 3 to explore associations between functional invertebrates and crop yield, and evaluates whether silvoarable systems can be a productive and financially viable alternative to arable monocultures.

Chapter 7 is a general discussion which aims to place the conclusions of the data chapters in a wider context, drawing overall conclusions as to how the adoption of agroforestry systems influences functional biodiversity and associated ecosystem services. The chapter also discusses the potential for agroforestry systems as a diversified farming system, summarises the findings in the context of answers to practical questions, and provides recommendations for further research.

2. Evaluating the effects of integrating trees into temperate arable systems on pest control and pollination

This chapter is derived from the following publication:

Staton, T., Walters, R.J., Smith, J., Girling, R.D. (2019) Evaluating the effects of integrating trees into temperate arable systems on pest control and pollination. *Agricultural Systems*, 176: 102676. https://doi.org/10.1016/j.agsy.2019.102676

Author contributions:

Conceptualisation: all authors; study design: all authors; formal analysis: TS; investigation: TS; data curation: TS; writing – original draft preparation: TS; writing – review and editing: all authors; visualisation: TS; supervision: RG; project administration: TS.

This chapter comprises a review and meta-analysis of the literature relating to invertebrate pests, natural enemies, and pollinators in silvoarable agroforestry systems in temperate regions. In addition, the discussion sets out a proposed framework for future research.

2.1 Abstract

Agroforestry systems, which incorporate trees into agricultural land, could contribute to sustainable agricultural intensification as they have been shown to increase land productivity, biodiversity and some regulating ecosystem services. However, the effect of temperate agroforestry systems on pest control and pollination services has not been comprehensively reviewed, despite the importance of these services for sustainable intensification. We review and analyse the available evidence for silvoarable agroforestry systems, following which we propose a predictive framework for future research to explain the observed variation in results, based on ecological theory and evidence from analogous systems. Of the 12 studies included in our meta-analysis of natural enemies and pests, the observed increases in natural enemy abundance (+24%) and decreases in arthropod herbivore/pest abundance (-25%) in silvoarable systems were both significant, but molluscan pests were more abundant in silvoarable systems in the two available studies. Only three studies reported effects on pollinators, but all found higher abundance in silvoarable compared with arable systems. Measures of pest control or pollination service are scarce, but suggest stronger effect sizes. Our framework seeks to establish hypotheses for future research through an interpretation of our findings in the context of the wider literature, including landscape characteristics, silvoarable system design and management, system maturity, trophic interactions and experimental design. The findings of this study suggest that silvoarable systems can contribute to sustainable intensification by enhancing beneficial invertebrates and suppressing arthropod pests compared with arable, but future research should include measures of pest control and pollination and implications for productivity and economic value.

2.2 Introduction

Global crop demand is rising rapidly, and is forecasted to increase by 100-110% from 2005 to 2050 (Tilman et al. 2011). The intensification of arable production in temperate regions has driven declines in biodiversity and associated ecosystem services, such as pest control and pollination (Bartomeus et al. 2014; Bianchi et al. 2006). This, has in many cases, led to a reliance on management techniques such as pesticide application, genetically modified crops and maintenance of managed honey bee colonies. The sustainability of such management practices is threatened by processes such as pesticide resistance (Sparks & Nauen 2015), secondary pest outbreaks (Dutcher 2007; Hill et al. 2017), depletion of non-renewable sources, environmental and human health risks associated with pesticides (Bernardes et al. 2015; Kim et al. 2017), and honey bee colony collapse or growth deficits (Aizen & Harder 2009; Neumann & Carreck 2010).

There is a strong and growing pressure to move towards more sustainable intensification of production, through harnessing natural processes to sustain productivity rather than relying on pesticides and managed pollinators (FAO 2013; Power 2010). One alternative tactic for reducing crop damage by pests is to enhance the effectiveness of their natural enemies, such as predators and parasitoids, by enhancing plant diversity and habitat complexity (Begg et al. 2017). This is the principle of conservation biological control (Barbosa 1998). Similar arguments have been proposed to encourage wild pollinators (Kovács-Hostyánszki et al. 2017; Woodcock et al. 2016), which have the potential to increase the effectiveness of pollination in flowering crops and mitigate against potential honey bee losses (Garibaldi et al. 2013; Hoehn et al. 2008).

One possible solution to the need for sustainable intensification is agroforestry, essentially 'the incorporation of trees into farming systems' (Gordon et al. 2018). Agroforestry has been proposed as a 'win-win' opportunity for productivity and environmental protection (The Woodland Trust 2018). Although more typical of the tropics due to lower constraints posed by mechanisation and climatic factors such as light availability, there is growing interest in this land use system in temperate regions because of its potential contribution towards sustainable intensification (Newman & Gordon 2018; Smith et al. 2012). For example, the 'establishment, regeneration or renovation of agroforestry systems' is promoted through the European Union's Common Agricultural Policy. Agroforestry is perceived as being beneficial for the environment and land stewardship, which are typically the main drivers for adoption (García de Jalón et al. 2018; Matthews et al. 1993).

Of particular interest in terms of the potential benefit from natural pest control and pollination is silvoarable agroforestry, which is the intercropping of trees or shrubs with arable crops (Fig. 2.1). Different methods of silvoarable production are practiced throughout northern temperate regions, sometimes being referred to by regional terminologies. These include tree-based intercropping and alley cropping systems in North America which typically use hardwoods for nut and timber production, and various agri-silviculture systems in the Himalayas (Newman & Gordon 2018). Timber is typically the main tree product produced in silvoarable systems, although intercropping with fruit trees is widely practised in China (Chang et al. 2018) and its potential for a quick return on investment is encouraging uptake in the UK (Newman et al.

2018). Silvoarable systems are far scarcer in southern temperate regions, although research platforms have been established (Newman & Gordon 2018). Temperate silvoarable systems have the potential to increase productivity compared with equivalent monocultures, for example Land Equivalent Ratios of between 0.98 and 1.37 have been estimated over the full tree rotation (Graves et al. 2010; Gruenewald et al. 2007).

Several reviews and meta-analyses have demonstrated that temperate agroforestry systems generally enhance biodiversity and some ecosystem services compared with arable cropping (Smith et al. 2013a; Stamps & Linit 1998; Torralba et al. 2016; Tsonkova et al. 2012). However, the effects of silvoarable systems on pest control and pollination services remain poorly understood in temperate regions; all but two of 42 studies included in a recent meta-analysis of pest, disease and weed control were conducted in the tropics and sub-tropics, which typically have different mechanisation requirements and utilise different tree/crop combinations to those used in temperate regions (Pumariño et al. 2015).

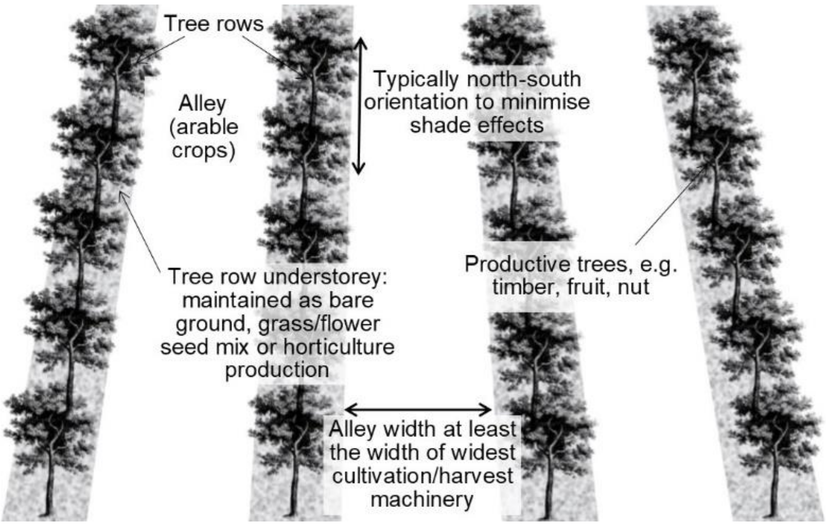

Figure 2.1. Illustration of a typical silvoarable alley-cropping system.

The aims of this review are to: 1) collate and analyse studies of pollinators, pests and their natural enemies in temperate silvoarable systems, specifically in terms of their potential contribution to pest control and pollination ecosystem services; and 2) develop a framework for future research to predict the factors which influence variation in results, with the aspiration of driving forward a unified research agenda.

2.3 Methods

Literature was sourced based on the following criteria (the selection process is summarised at Appendix 1):

1. A measure of abundance or activity density of invertebrate herbivores/pests, natural enemies or pollinators, and/or a measure of conservation biological control of animal pests and/or pollination were recorded;
2. Studies were undertaken in a temperate region, defined as latitude >40º north or south;
3. A silvoarable system, for this purpose defined as trees or shrubs incorporated into an arable field, was compared with an arable control, with the respective arable components comprising annual crops.

To minimise the risk of publication bias, we sourced both peer-reviewed and non-peer-reviewed literature, including theses and reports.

2.3.1 Data extraction

A total of 19 datasets were identified. We reviewed the characteristics of each study and the studied system(s), including sampling duration, alley width, system age, number of taxonomic orders studied and minimum distance between silvoarable and arable control plots. Capture or abundance data for natural enemies, pests (or herbivores where pest species were not specified), pollinators, and pest control proxies was sourced from each dataset to analyse effect sizes. Where necessary, data was extracted from figures using GetData Graph Digitizer (version 2.26, http://getdata-graph-digitizer.com). Any data collected from tree rows was excluded where possible to provide a comparison of silvoarable alleys versus arable. Where pitfall trap data from tree rows could not be excluded, the study/site was omitted entirely from the analysis of effect sizes, because the structural complexity of vegetation in tree rows could reduce capture rates (Melbourne 1999; Thomas et al. 2006). One study was completely excluded and one study partially excluded (two of the three sites) on this basis (Appendix 2).

2.3.2 Meta-analysis for herbivores/pests and natural enemies

To quantify the magnitude of effects for herbivores/pests and natural enemies, we calculated effect size as the log response ratio (Hedges et al. 1999) of mean functional group abundance in the silvoarable system versus the arable control. Hence, the response variables were herbivore/pest abundance and natural enemy abundance. The single explanatory variable was presence or absence of a silvoarable system.

Standard deviations could not be extracted for four of the 12 identified studies (Appendix 2), so were imputed based on their mean values (Lajeunesse 2013). Three of the four studies with missing standard deviations used pitfall trapping, therefore imputed standard deviations were calculated based on the significant linear relationship between mean and standard deviation for the two available pitfall trap studies with standard deviation data (Griffiths et al. 1998; Phillips et al. 1994). The significance of effects for herbivore/pest and natural enemy abundances were analysed in a mixed-effects meta-analysis model, using the rma.mv function of the 'metafor' package version 2.1-0 (Viechtbauer 2010) within R version 3.5.2 (R Core Team 2018). As multiple data points were extracted from some individual studies, study ID was included as a random effect. The results are reported as back-transformed values.

The imputation of standard deviations did not increase the risk of Type 1 errors, as effect sizes were reduced and p-values increased, compared with models which omitted studies with missing standard deviations. Outliers and influential observations were quantified using Cook's distance. For the pest/herbivores model, Cook's distance for a slug abundance data point was 0.30, compared with <0.05 for all other data points. Therefore, the results of a model excluding slug data (i.e. arthropods only) are also presented. For the natural enemies model, the data-point with the highest Cook's distance (0.13) was a negative effect size (i.e. lower abundance in the silvoarable plot than arable control) and was therefore retained to reduce the likelihood of a Type 1 error. Cook's distance was below 0.10 for all other data points. Publication bias was considered unlikely due to the inclusion of unpublished studies, but funnel plots were visually checked for symmetry. Heterogeneity, in the form of I^2 calculated from the models without random effects, ranged from 56% to 75%, lower than the median of 85% reported for ecological meta-analyses (Senior et al. 2016).

2.3.3 Review of other effect sizes

Effect sizes were calculated from five studies which reported a proxy for pest control, such as ratios of natural enemies to herbivores, pest mortality rates or pest parasitism rates, in a silvoarable system versus an arable control. Pollinator effect sizes were derived from three studies which reported abundances in silvoarable systems and arable controls. To investigate whether the functional group responses are highly influenced by any specific taxa, effect sizes were also calculated for taxa which were included in three or more studies (Araneae, Carabidae, Coccinellidae, Syrphidae and Aphididae). We calculated effect size as the mean abundance (or for pest control proxies, the mortality/parasitism rate or ratio of natural enemies to pests) in the silvoarable system, divided by the respective value for the arable control. Due to the low number of available studies for these measures, pooled effect sizes were not analysed. Finally, four studies reported some measure of crop damage or yield, which we describe in the Results.

2.3.4 Predictive framework

Our findings were used to inform and construct a predictive framework for future research, which identifies a series of hypotheses to predict the factors which influence variation in the results. The components of the framework were selected based on a wider review of ecological theory and analogous systems, such as hedgerows, field margins, flower strips and beetle banks.

2.4 Results

2.4.1 Characteristics of studies

A total of 19 datasets were extracted from 17 studies undertaken in five countries, comprising Canada, France, Turkey, UK and USA, with publication dates ranging from 1993 to 2015. Data from the majority of the studies included in our analysis were taken from single sites over less than two years (Fig. 2.2a). There was a strong bias towards systems with alley widths of around 12 m (Fig. 2.2b). Most of the studied systems were relatively young in age, i.e. less than ten years since planting (Fig. 2.2c). The majority of studies report on the abundances of three or fewer taxonomic orders, with only two studies reporting on seven or more orders (Fig. 2.2d). Where the minimum distance between the silvoarable and arable plots is specified, this was typically <50 m (Fig. 2.2e, three outliers are not shown).

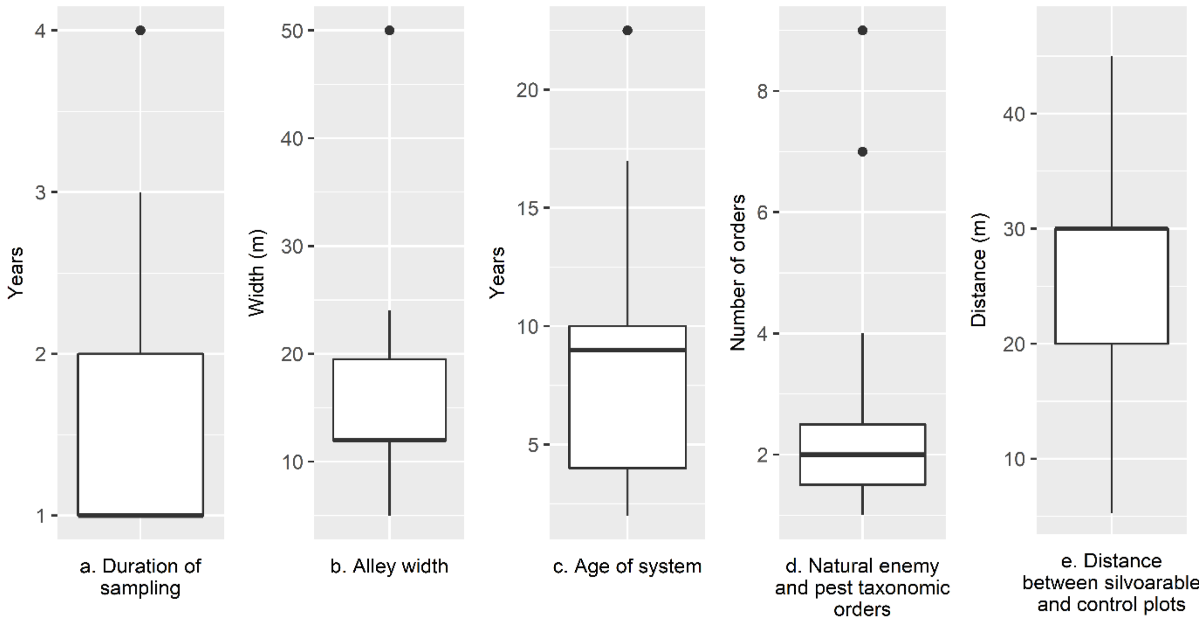

Figure 2.2. Characteristics of studies of invertebrate pest control and pollination in temperate silvoarable systems, where the relevant information was specified. For studies of multiple sites, each site is represented individually. Multiple studies reporting on the same data are represented once collectively. Each 'box' represents the first and third quartiles, whilst the 'whiskers' extend to the largest/smallest value no further than 1.5 * inter-quartile range from the box. Three outliers are not plotted in Fig. 2.2e (130 m, 210 m and 270 m), but are included in the calculations.

2.4.2 Herbivores/pests and natural enemies: meta-analysis

Invertebrate herbivore/pest abundances were lower in the silvoarable compared with arable systems, with a back-transformed mean effect size of 0.89 (Fig. 2.3), but this was not significant (z=-0.650, p-value=0.516). However, the abundance of arthropod herbivores/pests was significantly lower in the silvoarable than arable systems (z=-2.005, p-value=0.045), with a mean effect size of 0.75 (Fig. 2.3). This contrasts to slug abundance, which was higher in the silvoarable than arable systems, with effect sizes of 1.12 to 1.53 across the two studies. Natural enemy abundance was significantly higher in silvoarable compared with arable systems (z=2.528, p-value=0.011), with a mean effect size of 1.24 (Fig. 2.3). Only one of the nine natural enemy effect sizes was less than one (Appendix 2).

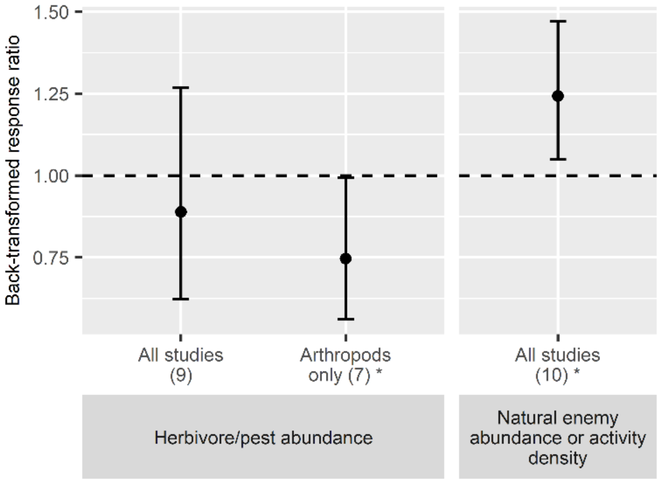

Figure 2.3. Means and confidence intervals of the back-transformed response ratios of invertebrate herbivore/pest and natural enemy abundance in silvoarable alleys (treatment) versus arable fields (control). A response ratio of >1 indicates a higher abundance in the silvoarable than the arable system. Numbers in parentheses represent the number of studies and '*' denotes significance (p-value < 0.05). Data is provided in Appendix 2.

Data from four sites reported in two studies were not included in the effect size analysis because pitfall trap data from tree rows and alleys could not be separated. In these studies, natural enemy activity was lower in the silvoarable system than the arable control at three of the four sites, whilst the study which also sampled slugs found higher captures in the silvoarable than the arable system at one site but lower captures in the silvoarable system at the other site (Appendix 2).

2.4.3 Proxies for pest control

One measure of pest control is the ratio of the number of natural enemies to herbivores/pests. Two studies found a higher ratio in silvoarable versus arable systems (Table 2.1), which could be seen as a proxy for higher pest control. Three datasets included mortality or parasitism rates of pests, and all found consistently higher rates in silvoarable systems compared with arable systems (Table 2.1), again suggesting a higher level of pest control.

Table 2.1. Summary of studies which reported proxies for pest control, i.e. ratios of airborne natural enemies to herbivores or pest mortality/parasitism rates. Effect sizes are calculated as the silvoarable ratio/rate divided by the respective arable control value.

Reference	**Proxies for pest control**	**Silvoarable**		**Arable**		**Effect size**	**Tree row data excluded?**
		Ratio	**%**	**Ratio**	**%**		
Peng et al. (1993)	Ratio of airborne natural enemies to herbivores	1.46	-	1.15	-	1.27	Yes
Howell (2001)	Ratio of airborne predators to herbivores	1.79	-	1.37	-	1.31	No
	Ratio of airborne parasitoids to herbivores	2.94	-	1.08	-	2.72	
Stamps et al. (2009a)	Alfalfa weevil mortality rate	-	33.85	-	28.26	1.20	Yes (not sampled)
(Naeem et al. 1994, 1997)	Aphid parasitism rate	-	2.81	-	1.66	1.69	Yes
(Muhammad et al. 2005)	Aphid parasitism rate	-	12.8	-	7.6	1.68	Yes (not sampled)

2.4.4 Pollinator abundance

Only three studies, in the UK and Canada, reported abundances of pollinating insects in silvoarable systems and arable controls. Effect sizes ranged from 1.17 to 2.55, indicating beneficial effects on pollinator populations in silvoarable systems compared with arable controls (Table 2.2), but study replication was low. One study also reported higher California Poppy phytometer seedset by a factor of 4.5 in agroforestry compared with arable systems (Table 2.2).

Table 2.2. Effect sizes for studies which reported pollinator abundances or pollination service, calculated as pollinator abundance or seedset in the silvoarable system divided by the respective value in the arable control.

Reference	Taxa / measure of service	Effect size	Tree row data excluded?
Peng et al. (1993)	Syrphidae, *Bombus*	1.17	Yes
Howell (2001)	Andrenidae, Apidae, Colletidae, Halictidae, Megachilidae	1.72	No
Varah (2015): 2 sites	Syrphidae, *Bombus* (solitary bees excluded as silvoarable data not separable from silvopasture data)	2.55	No
	Seedset in *Eschscholtzia californica* phytometers (across two silvoarable and one silvopasture site, not separable)	4.5	No

2.4.5 Taxon-specific effects

The results were also analysed for aphids and four taxa of predators comprising Araneae, Carabidae, Coccinellidae and Syrphidae. The effect sizes were highly variable, ranging below and above 1 in four of the five taxa analysed (Table 2.3). The only taxon represented by at least three studies which had consistently higher numbers in silvoarable systems compared with arable controls was hoverflies (Syrphidae).

2.4.6 Implications for crop damage and yield

Evidence of crop damage by invertebrate pests is very limited, and only two studies have attempted to establish a link between pest control and yield of the arable component. Griffiths et al. (1998) recorded higher slug damage to a pea crop in a UK silvoarable system compared with an arable control, with damage level positively correlated to slug captures. However, yield was not measured. In Turkey, Akbulut et al. (2003) observed a lower level of crop damage from invertebrates in silvoarable plots, accompanied by higher yield of beans but lower yield of maize, relative to arable. Other studies have simultaneously sampled cereal yields and invertebrates in silvoarable systems, finding lower yields in silvoarable compared with arable in conventional systems (Burgess et al. 2003), and the opposite result in organic systems

(Varah 2015), but disentangling the effect of pest control or pollination on yield from other factors, notably tree-crop interactions such as shade, is problematic.

Table 2.3. Effect sizes for five of the most commonly studied taxa in temperate silvoarable systems, calculated as total or mean abundance in the silvoarable system divided by the respective value in the arable control. Syrphidae only include species with predatory larvae.

Reference	**Effect size**				
	Natural enemies				**Herbivores / pests**
	Araneae	**Carabidae**	**Coccinellidae**	**Syrphidae**	**Aphidoidea**
Peng et al. (1993)	1.35 (airborne)	-	0.25	1.22	1.77 (all species)
Phillips et al. (1994)	-	0.83	-	2.64	-
Peng and Sutton (1996)	1.22	1.12	3.2	-	
Naeem et al. (1994, 1997)	-	-	-	-	0.53 (one species)
Howell (2001)	0.95 (airborne)	9 (airborne)	0.5	1.51	0.26 (all species)
Burgess et al. (2003): Leeds site	0.65	0.73	-	-	-
Muhammad et al. (2005)	-	-	-	-	0.45 (one species)
Smits et al. (2012)	-	-	-	-	1.01 (three species)
Sharman (2015)	-	1.54	-	-	-

2.5 Discussion

2.5.1 Effects of temperate silvoarable systems on pest control and pollination

Invertebrate herbivores / pests

Our analysis demonstrates a reduced arthropod herbivore abundance in silvoarable alleys than in arable control conditions. This is consistent with the resource concentration hypothesis, which predicts that specialist herbivores, i.e. those with a narrow host range, should be less abundant in a more diverse system than a monoculture of its host plant, due to the masking of host chemical cues (Root 1973). This hypothesis does not however extend to generalist pests such as slugs, for which we find evidence of higher abundance in silvoarable systems relative to arable controls, although these results were derived from only two sites. Similar effects have been reported in and adjacent to flower-rich field margins (Eggenschwiler et al. 2013; Frank 1998), which suggests that areas which provide a refuge from tillage could boost slug populations.

Natural enemies

The findings indicate that the natural enemies of pests are more abundant in silvoarable alleys compared with arable systems, although there are no clear differences in responses among natural enemy taxa. The benefit to natural enemies could be explained by the resources provided by silvoarable systems. For example, undisturbed tree rows could provide overwintering refugia, which have been shown to be important for the maintenance of ground-based natural enemy populations in other systems (Landis et al. 2000; Öberg et al. 2008; Varchola & Dunn 2001). Silvoarable systems could also enhance fine-scale complexity which has been shown to benefit parasitoids (Chaplin-Kramer et al. 2011; Thies et al. 2005), whilst tree rows could provide alternative food sources often required by this functional group (Dyer & Landis 1996; Murphy et al. 1998; Pfannenstiel et al. 2010).

Pollinators

Although study replication was low, the observed increase in pollinator abundance in silvoarable systems compared with arable controls is consistent with the demonstrated benefits of flowering strips and hedgerows (Garratt et al. 2017; Morandin & Kremen 2013; Nicholls & Altieri 2013). This could be explained by the sheltered microclimate in silvoarable systems, in addition to the potential for flowering resources in silvoarable tree rows, including the understorey. The uncultivated tree rows could also provide nesting opportunities for pollinators, as demonstrated by a previous modelling exercise which predicted that nesting bee abundance would be increased by adopting silvoarable systems at a landscape scale (Graham & Nassauer 2019).

Magnitude of effects

Our reported mean effect sizes of 1.24 and 0.75 on natural enemy and arthropod herbivore/pest abundances respectively are similar to those reported from meta-analyses of other field scale enhancements such as polycultures, orchard vegetation management and global (predominantly tropical) agroforestry, which range from 1.11 to 1.50 for natural enemies, and 0.68 to 0.78 for pests (Iverson et al. 2014; Pumariño et al. 2015; Winter et al. 2018). These effect sizes are, however, considerably smaller than those typically observed for complex landscapes with a high proportion of non-crop habitats where, taking natural enemy abundance as an example, the majority of studies report effect sizes of at least 2 compared with simple large-scale landscapes (Bianchi et al. 2006).

Effects on pest control and pollination services

We find limited evidence of effects on pest control or pollination services, although there is some evidence for higher ratios of airborne natural enemies to herbivores, pest mortality and parasitism rates in silvoarable compared with arable systems. This limited evidence does however support the expectations of Stamps and Linit (1998), who recognised the theoretical potential for agroforestry systems to benefit pest control through plant diversification. Evidence for corresponding effects on crop damage or yield is scarcer still, with contradictory evidence, whilst evidence for pollination service is limited to a finding of higher California Poppy seedset in silvoarable compared with arable systems across two sites (Varah 2015). The economic implications of pest control and pollination in silvoarable systems have yet to be assessed.

2.5.2 A proposed framework for future research

Agroforestry research in general is constrained by the suitability of appropriately scaled field sites designed for experimental vigour with proper controls (Stamps & Linit 1999), which poses unique challenges to evaluating the factors which influence variation in effects. We therefore propose a framework to predict how these factors influence the observed abundances of natural enemies, pests and pollinators in temperate silvoarable systems (Fig. 2.4). For each identified factor which could influence variation, we refer to evidence from the studies included in our analysis and, as these are limited, ecological theory and evidence from analogous systems, where available, to form a series of hypotheses which can be tested by future research.

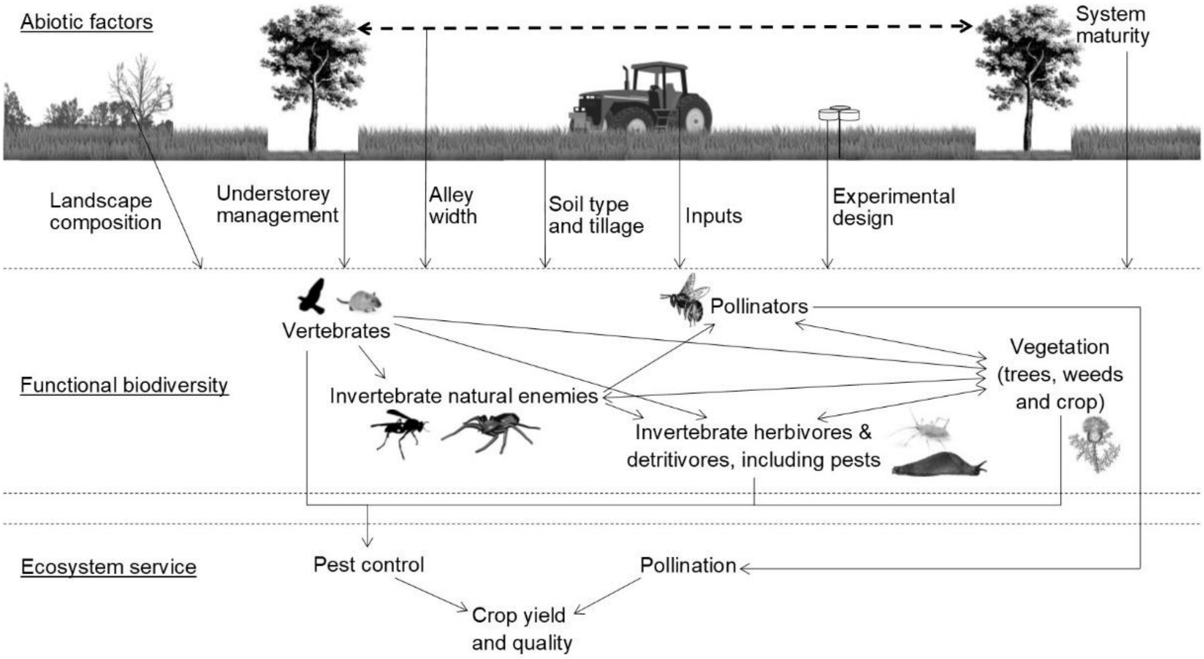

Figure 2.4. Illustrative summary of the key factors predicted to influence functional biodiversity in temperate silvoarable systems, the major interactions between functional groups and their contribution to pest control and pollination.

Soil type and tillage

Although direct evidence is lacking, soil type could be critical in the outcome of pest control based on the evidence for slug problems in silvoarable systems. For example, a major slug pest, *Deroceras reticulatum*, favours fine-textured soils with high moisture content (Ondina et al. 2004), suggesting that silvoarable systems on such soil types could be prone to higher pest damage. Further research could investigate whether adapting soil cultivation in silvoarable systems could help mitigate this damage, for example, by modifying tillage depth, timing and/or frequency (Roger-Estrade et al. 2010).

Inputs

Our findings of enhanced natural enemy activity and reduced pest pressure in silvoarable alleys compared with arable controls suggest that pesticide inputs in non-organic systems could potentially be reduced without compromising productivity, as demonstrated for hedgerow restoration (Morandin et al. 2016). Furthermore, an enhanced level of pest control in organic silvoarable systems compared with arable controls could reduce crop loss to pests. These hypotheses warrant further investigation.

Alley width

Alley width is typically constrained by the size of machinery in temperate regions. Although there is a strong bias in the literature towards systems with alley widths of around 12 m (Fig. 2.2b), three studies included in our analysis found that tree rows or the edges of crop alleys support greater abundances of natural enemies and lower pest abundances than the centre of crop alleys (Peng et al. 1993; Phillips et al. 1994; Rekany 2015). Furthermore, stronger distribution patterns of predators have been observed in 50 m crop alleys compared with 24 m alleys (Rekany 2015). This broadly corresponds to studies of woody field boundaries, which find highest abundances of natural enemies and pollinators at around 2 to 10 m from the boundary, before rapidly declining (Lewis 1969; Morandin et al. 2014). Future research could therefore test whether narrow alley widths have the greatest benefit on pollination and natural enemy activity.

Understorey management

Two of the studies included in our analysis compared vegetated understoreys with chemically weeded understoreys. A study of aphid natural enemies found no effect between treatments, possibly because the vegetated treatment did not properly establish (Smits et al. 2012). However, Burgess et al. (2003) captured fewer slugs and more spiders in alleys adjacent to vegetated versus bare understoreys, suggesting that understorey vegetation promotes pest control, although there was little difference in carabid beetle captures between treatments. Nevertheless, management of silvoarable tree rows to promote tussock-forming grasses could replicate the benefits of beetle banks (Collins et al. 2003), which is worthy of further investigation.

In addition, evidence from flower strips shows that mixes rich in pollen and nectar are most beneficial to pollinators, whilst natural enemies appear to be less strongly associated with vegetation type (reviewed in Haaland et al. 2011). Nevertheless, flower strips designed to benefit natural enemies of wheat pests have been successful in reducing pest pressure (Tschumi et al. 2015). A similar tailored approach could be investigated in silvoarable systems.

Maturity

The longest-running study in our analysis found that the slug population increased over the course of four years in a young silvoarable system compared with a control plot (Griffiths et al. 1998), whilst the abundance and/or diversity of birds and small mammals have also been shown to increase with system maturity (Gibbs et al. 2016; Klaa et al. 2005). Conversely, the abundance and diversity of epigeal invertebrate predators showed no significant response to field margin and hedgerow age in the UK, suggesting rapid colonisation, although some species were more closely associated with mature habitat (Pywell et al. 2005). We recommend that this could be investigated through long-term studies of invertebrate communities in silvoarable systems.

Vegetation

Two of the studies included in our analysis considered diversity and abundance of vascular plants in silvoarable versus arable systems, finding higher plant species richness in silvoarable alleys (Varah 2015) and greater cover of non-crop plants, especially adjacent to vegetated understoreys, possibly due to seed-spread during cutting (Burgess et al. 2003). In contrast, lower numbers of weeds were found in a silvoarable system in France relative to an arable control early in the season, despite a higher species richness in the silvoarable system (Meziere et al. 2016). This contrast among studies could be explained by the differing abilities of weed species to ingress from perennial habitats (Marshall 2004). Therefore, we would predict that weed problems in silvoarable systems will be highly context-dependent. Weed cover could also provide a mechanism for the observed benefits on natural enemies and pollinators in silvoarable systems, as demonstrated by a positive association of carabid beetle activity with weed cover in one of the studies in our analysis (Sharman 2015).

The choice of tree species could influence micro-climatic conditions and provide resources such as nectar for functional groups. Studies of hedgerows and agroecosystems generally show that plant diversity enhances natural pest control and pollination services (Garratt et al. 2017; Isbell et al. 2017; Letourneau et al. 2011), and we would predict this to apply to silvoarable systems. On the contrary however, interplanting shrubs within apple tree rows did not influence pest or natural enemy communities in one silvoarable system (Kranz et al. 2019), although confirmatory evidence is needed from other sites to improve our understanding of the influence of tree species and diversity on pest control and pollination.

The choice of arable crop may also influence results, for example, the study with the weakest effect size for pollinators was of a pea crop, possibly because of the attractant effect of the mass-flowering resource in the control plot compared with studies based on cereal crops. Long-term and/or multiple-site studies would further test this hypothesis.

Trophic interactions among fauna

In general, the efficacy of conservation biological control is dependent on synergistic or antagonistic interactions between natural enemies (Straub et al. 2008; Thies et al. 2011), whilst predation of pollinators could reduce fruit set (Dukas 2005). Few studies in our analysis considered these interactions, although positive correlations have been demonstrated between spiders and carabid beetles in a North American silvoarable system, suggesting limited interference (Stamps et al. 2009b).

Interactions between vertebrates and invertebrates could also play a role in pest control and pollination, particularly given the potential benefits of silvoarable systems on vertebrate populations. A literature search on vertebrates in temperate silvoarable systems yielded five additional studies, which reported increased abundance and/or species richness of small mammals (Klaa et al. 2005; Wright 1994), bats (Disca 2003) and birds (Gibbs et al. 2016;

Williams et al. 1995) in silvoarable versus arable systems. Vertebrates could benefit pest control through direct predation of pests (e.g. Kunz et al. 2011; Whelan et al. 2008). On the other hand, vertebrates could directly cause pest problems, for example crop damage arising from roe deer, rabbits, wild boar and pigeons have been anecdotally reported in silvoarable systems (Gosme 2014; Newman et al. 2018; Smith et al. 2016). Vertebrates could also disrupt natural enemy functionality (Martin et al. 2013), for example, an apparent increase in rats correlated with a substantial decrease in carabid beetle abundance in a silvoarable system (Stamps et al. 2009b). Interactions are therefore an important avenue for further research given their implications for pest control and potentially pollination.

Landscape composition and complexity

Two of the studies included in our analysis identified that proximity to treed landscape features (forestry plots or boundary hedgerows) outside of the silvoarable system influenced their results, benefitting pest parasitism and pollinator abundance respectively (Muhammad et al. 2005; Varah 2015). The study with the second-lowest calculated effect size of natural enemy abundance noted that the diversity of the surrounding landscape may have masked any benefit of the silvoarable system (Smits et al. 2012), whilst a well-studied system in an intensive agricultural landscape had relatively strong effect sizes for natural enemies and pollinators (Rekany 2015; Sharman 2015; Varah 2015). This is supported by landscape-scale studies of pest control and pollination, which suggest that functionality is high in diverse landscapes (Holzschuh et al. 2007), such that field-scale enhancements are more likely to be effective in simple landscapes, defined as 1-20% of non-crop habitat (Tscharntke et al. 2005). Although this hypothesis would be difficult to vigorously test in silvoarable systems, a standardised experimental design across a network of sites with similar characteristics but differing landscape context would help to predict those landscapes in which silvoarable systems would be most effective in terms of natural pest control and pollination.

Experimental design

Our results show that effect sizes in silvoarable systems tend to be relatively small compared with landscape-scale studies, and so experiments should be designed to have sufficient power to detect effect sizes of 10 to 30 % (Fig. 2.3). Experimental design and analysis should take limitations of survey techniques into account, for example, the inclusion of pitfall trap data collected from tree rows with complex understoreys in comparisons between silvoarable and arable systems could bias results against silvoarable systems (Thomas et al. 2006), as indicated by our analysis (Appendix 2). Differences between the silvoarable and arable control plots could also influence results, particularly differences in historical land use, environmental conditions (including soil type), crop selection, management, proximity to landscape features and proximity between treatment and control plots.

2.5.3 Study limitations

Our analysis of pests, natural enemies and pollinators focusses on invertebrates, as other taxa have been scarcely studied in temperate silvoarable systems and predicting their net effect on pest control and pollination is often more complex than for most invertebrates. Nevertheless, we consider plants and vertebrates and their potential implications for pest control and pollination in our predictive framework above.

Pests of the arable crop component of silvoarable systems are the focus of the study, rather than pests of the tree component which have been scarcely studied. Nevertheless, there is some evidence that aphid densities are lower in silvoarable tree rows than in forestry controls (Naeem et al. 1997; Naeem & Compton 2000). Two studies have referred to pest damage in silvoarable apple trees compared with orchards, although results are inconclusive and appear to vary according to pest taxa and fruit stage (Kranz et al. 2019; Smith et al. 2014).

Our analysis pools together numbers of captures/observations for different taxa recorded in each study, therefore, numerically abundant species are well represented in effect sizes compared with less abundant species, regardless of their body size or effect on pest control or pollination. Given that small sized carabid beetles were trapped at higher abundance in silvoarable compared with arable systems, in contrast to large generalist species (Rekany 2015), accounting for body size could reduce effect sizes, although the situation is complex as larger carabid species could also predate smaller carabids (e.g. Prasad & Snyder 2006), thereby antagonising pest control.

The analysis of pooled numbers of captures/observations does not take diversity into account, as only two of the studies report on diversity of functional groups, finding significantly higher diversities of invertebrate predators, herbivores and parasitic Hymenoptera in silvoarable relative to arable systems (Howell 2001; Stamps et al. 2002).

Whilst our analysis goes some way to comparing pests, natural enemies and pollinators in silvoarable systems compared with arable, more research is needed to quantify subsequent effects on pest control and pollination service outcome.

2.5.4 Conclusion

We find evidence for significantly enhanced natural enemy populations and significantly suppressed arthropod herbivore populations in silvoarable systems, but molluscan pests were more numerous in the two available studies, compared with arable. Pollinators were also more abundant in silvoarable than arable systems, but study replication was low. This suggests a higher efficacy of pollination and natural pest control in silvoarable crop alleys compared with arable systems, although crop damage from slugs could cause problems on some farms. Our findings therefore provide further support for the role of silvoarable systems in sustainable intensification, in conjunction with the demonstrated benefits to other ecosystem services (e.g. Smith et al. 2013a; Torralba et al. 2016; Tsonkova et al. 2012). Nevertheless, further well-replicated empirical research or modelling studies are required to test our predictive framework of the factors which influence pests, natural enemies and pollinators in silvoarable systems, in addition to measures of pest control and pollination, and their implications for productivity, economic output and resilience.

2.6 Data availability

Additional information on the attributes of the reviewed literature is available in Supplementary Material to the published article (https://doi.org/10.1016/j.agsy.2019.102676).

3. Evaluating a trait-based approach to compare natural enemy and pest communities in agroforestry versus arable systems

This chapter is derived from the following publication:

Staton, T., Walters, R.J., Smith, J., Breeze, T.D., Girling, R.D. (2021) Evaluating a trait-based approach to compare natural enemy and pest communities in agroforestry vs. arable systems. *Ecological Applications*, 31(4): e02294. https://doi.org/10.1002/eap.2294

Author contributions:

Conceptualisation: all authors; study design: all authors; data collection: TS; formal analysis: TS; investigation: TS; data curation: TS; writing – original draft preparation: TS; writing – review and editing: all authors; visualisation: TS; supervision: RG; project administration: TS.

This is the first chapter which is based on new empirical data, and presents the results of biodiversity data collected from agroforestry field sites with paired arable controls, focussing on plants, invertebrate herbivores and pests, and natural enemies. In this chapter, a trait-based analytical approach is compared with a traditional taxonomic approach.

3.1 Abstract

Diversified farming systems, for example those that incorporate agroforestry elements, have been proposed as a solution that could maintain and improve multiple ecosystem services. However, habitat diversification in and around arable fields has complex and inconsistent effects on invertebrate crop pests and their natural enemies. This hinders the development of policy recommendations to promote the adoption of such management strategies for the provision of natural pest control services. Here, for the first time we conducted a trait-based approach to investigate the effect of farming system on plant, invertebrate herbivore and invertebrate natural enemy communities. We then evaluated this approach by comparing the results to those generated using a traditional taxonomic approach. At each of three working farms, we sampled within an agroforestry field (a diverse farming system comprising alleys of arable crops separated by tree rows), and within a paired non-diversified area of the farm (arable control field). Each of 96 sample points was sampled between eight and ten times, yielding 393,318 invertebrate specimens from 344 taxonomic groups. Diet specialisation or granivory, lack of a pupal stage, and wing traits in invertebrates, along with late flowering, short flowering duration, creeping habit and perenniality in plants, were traits more strongly associated with agroforestry crop alleys than the arable control fields. We hypothesise that this is a result of reduced habitat disturbance and increased habitat complexity in the agroforestry system. Taxonomic richness and diversity were higher in the agroforestry crop alleys compared with the arable control fields, but these effects were stronger at lower trophic levels. However, functional trait diversity of natural enemies was significantly higher in the agroforestry crop alleys than the arable control fields, suggesting an improved level of biocontrol, which was not detected by traditional diversity metrics. Of eight key pest taxa, three were significantly suppressed in the agroforestry system, whilst two were more abundant, compared with the arable control fields. Trait-based approaches can provide a better mechanistic understanding of farming system effects on pests and their natural enemies, therefore we recommend their application and testing in future studies of diversified farming systems.

3.2 Introduction

Sustainable intensification of agriculture, or ecological intensification, has been proposed as a nature-based solution to meet food production demands by utilising ecosystem services, such as natural pest control, rather than depending solely on external inputs (Bommarco et al. 2013; Garnett et al. 2013). For example, natural landscape elements and diversified farming systems have been proposed as an effective means of encouraging the predators and parasitoids (i.e. natural enemies) of invertebrate pests, which could help reduce the current reliance on pesticides for agricultural production (e.g. Attwood et al. 2008; Bianchi et al. 2006; Landis et al. 2000). Recently however, there has been growing recognition that the responses of invertebrate natural enemies and pests to diversification are complex and depend on taxa and context, such as landscape configuration and diversity, farm management, and climate (Karp et al. 2018; Straub et al. 2008; Tscharntke et al. 2016). This results in a major obstacle for the development of policy recommendations to promote the adoption of agricultural management strategies for natural pest control. The uptake of such strategies remains very limited (Kleijn et al. 2019) and growers are sometimes fearful that they might exacerbate pest problems (Chaplin-Kramer et al. 2019).

One method proposed to enhance our understanding of the mechanisms and biotic processes that underpin the complex responses of invertebrate pests and their natural enemies to diversification is a functional trait-based approach (Jonsson et al. 2017; Perović et al. 2018; Wood et al. 2015). Here, biological communities are described in terms of their mean trait values or trait diversity rather than their taxonomic identities, on the premise that an individual's response to, or effect on, the environment is influenced primarily by traits such as feeding specialisation, dispersal tendency and hunting mode (Perović et al. 2018). This trait-based approach has the potential to move our understanding away from context- and taxon-specific case studies to a more general, mechanistic and predictive framework (Wood et al. 2015).

The application of trait-based approaches to agro-ecosystems has therefore been identified as an urgent research need (Karp et al. 2018; Perović et al. 2018; Wood et al. 2015). While trait-based approaches have been widely used to understand ecosystem functions and dynamics in plant and soil invertebrate ecology (e.g. Faucon et al. 2017; Lavorel 2013; Pey et al. 2014), recent applications suggest they can also shed light on the complexity of functional biodiversity responses to landscape composition and configuration (Martin et al. 2019), and explain the effect of natural enemies on prey suppression through functional trait diversity (Greenop et al. 2018).

A diversified farming system that is receiving revived interest in the context of ecological intensification of agriculture is agroforestry, which is loosely defined as farming with trees. For example, agroforestry is now promoted by the European Union’s Common Agricultural Policy (Article 23 of Regulation 1305/2013) and by the United States Department of Agriculture (2019). This promotion is in part on the basis of evidence of improved productivity and regulating ecosystem services (e.g. Torralba et al. 2016; Waldron et al. 2017). Agroforestry systems have some ecological analogies to hedgerows, grass strips and flower strips, but the productivity of the tree rows allows for a much greater density, and increased longevity, of perennial vegetation strips within a field. Therefore, agroforestry systems have the potential to deliver an even greater enhancement of natural enemies and suppression of invertebrate pests compared to other types of perennial vegetation strips (e.g. Collins et al. 2002; Hatt et al. 2017). However, the considerable variation in results among studies of agroforestry systems to-date suggests that effects on natural pest control could be dependent on taxon and/or context (Pumariño et al. 2015; Staton et al. 2019).

Trait-based approaches have recently been applied within an agroforestry system in France to understand the spatial patterns of plant and winter carabid beetle communities. Carabid beetle traits that were more associated with tree rows than adjacent arable crop alleys included large body size, granivorous diet and adult overwintering, which were explained in terms of sensitivity to agricultural disturbance (Boinot et al. 2019b). The authors hypothesised that this could result in greater trait complementarity in arable alleys within agroforestry systems in comparison to arable fields, potentially leading to enhanced biological control of a wider range of prey taxa, including weeds. Perennial, rhizome- or stolon-spreading plant species were better able to disperse into arable crop alleys from tree rows, although weed/crop ratios were similar and non-significant between agroforestry crop alleys and arable control fields (Boinot et al. 2019a). However, this trait-based approach has not yet been applied to compare invertebrate and plant communities within agroforestry systems to those in non-diversified arable fields.

Therefore, in this study, we adopt this trait-based approach and compare it to a traditional taxonomic approach to investigate the effect of field-scale agroforestry systems versus non-diversified arable fields on communities of plants, invertebrate herbivores and invertebrate natural enemies. We selected experimentally robust sites with well paired arable control fields, and maximised temporal replication to generate a representative dataset for the main duration of insect activity during each year. We therefore sampled on eight to ten occasions over two years across three working farms (see Appendix 3 for photos and further details). Each farm contained a paired agroforestry system and an arable control field, both of which were under the same management regime. This field-scale approach allowed us to realistically sample community interactions under field conditions (Kleijn et al. 2019). This is particularly important for functional trait studies which are potentially strongly scale-dependent (Wood et al. 2015).

The agroforestry systems at our study sites were all based on an innovative design, comprised of fruit trees (predominantly apple) intercropped with a cereal-based rotation. This system aims to maximise productivity and multiple ecosystem services (Smith et al. 2016), and whilst they are currently rare globally, interest and uptake is increasing in the UK (Newman et al. 2018).

In this study we aim to test the effect of farming system (agroforestry versus arable) on (1) trait and taxonomic-identity community composition for each of three trophic levels (plants, invertebrate herbivores and invertebrate natural enemies), (2) diversity metrics, including taxonomic richness and Shannon diversity across trophic levels and, for natural enemies, phylogenetic and functional diversity of effect traits, and (3) a series of key pest taxa with differing trait profiles.

3.3 Methods

3.3.1 Field sites

Three field sites, located in East Anglia and the East Midlands of the UK, were selected on the basis that each possessed a similar type of agroforestry system and a non-diversified arable control field under the same farm management and crop rotation. This allowed us to control for confounding factors, such as management and landscape context, between farming systems as far as possible whilst sampling within realistic field-scale conditions. All sites were working farms; two were organic while the third was conventional and minimum-tillage. Crop rotations were based around cereals, plus oilseed rape at the conventional farm. The agroforestry fields were based on the innovative silvoarable system introduced at Whitehall Farm, Cambridgeshire in 2009 (Newman et al. 2018). In this system, arable crop alleys (24 m in width) are intercropped with 3-4 m wide tree rows, which predominantly contain apple trees on semi-dwarf rootstocks. Depending upon the farm, the agroforestry trees were planted in late 2009, early 2014 or early 2015. Further information is provided in Appendix 3.

3.3.2 Experimental design

Two crop alleys were sampled in the centre of an agroforestry field at each site. Eight sample points were distributed at set distances from the tree row across each alley, including two points in each adjacent tree row, and were randomly staggered parallel to the tree row (Appendix 4). Therefore, there were 16 sample points in the agroforestry field at each site. The same sampling arrangement was repeated in a non-diversified arable field at each site to act as a control. Therefore, across all sites there was a total of 96 sample points. All samples were located at least 30 m from the nearest field boundary to minimise the influence of edge effects.

Samples were collected from May to October 2018, and April to November 2019. A variety of techniques were employed at each sample point to target different elements of the plant and invertebrate communities. These comprised pitfall traps to sample ground-based invertebrates, pan traps to sample aerial insects, crop assessments to count aphid numbers, and quadrats (excluding tree rows) to record non-crop plant species and their coverage. Pitfall trap capture rates are a measure of activity-density, and differed markedly between tree rows and arable crop alleys, including just 1.5 m away from the tree rows. This was probably due to the higher vegetation complexity in the tree rows reducing movement activity (Thomas et al. 2006). Pitfall trap samples from tree rows were therefore not included in the analysis, because of this apparent source of bias. Damaged traps were not included in the analysis, which amounted to 50 of 756 pitfall trap samples and 19 of 864 pan trap samples (Appendix 4). At each site, pitfall traps were sampled eight to ten times over the two years, pan traps nine times, quadrats twice (i.e. once per year), and aphid crop assessments once in July 2019. Further information on sampling methodology is provided in Appendix 4. All specimens (except Collembola in 2018) were identified to establish trophic level, which required varying taxonomic resolution (Appendix 5).

3.3.3 Data analysis

Three trophic levels were considered in the analysis, comprising plants, herbivorous invertebrates, and natural enemy (predator or parasitoid) invertebrates. Each taxon was assigned a trophic level based on information in the literature (see ‘Data Availability’ section). Pitfall trap data was adjusted to provide mean captures per day. Exploratory analysis was initially undertaken separately for pitfall and pan trap datasets, however no consistent differences in effects of farming system on trait profiles were apparent between the sampling methods. Therefore, both datasets were analysed together for the invertebrate community analyses (Sections 3.4.1 and 3.4.2) to investigate overall effects at the trophic level, which meant that tree row data was excluded (as discussed above). Due to field sampling constraints, in some cases pitfall and pan trap samples were collected in different months. In these cases, to simplify the data structure, pan trap samples were re-assigned to the nearest pitfall trap month, which never exceeded one month and a day. All analyses were undertaken in R version 3.5.2 (R Core Team 2018).

Comparing traits to taxonomic identities

We selected traits based on those hypothesised to underpin community responses to environmental and trophic effects (Greenop et al. 2018; Perović et al. 2018; Storkey et al. 2013), particularly in the context of agroforestry (Boinot et al. 2019a, b). Traits were not selected if they were unknown for a high proportion of specimens. For plants, five continuous and three categorical traits were selected, while seven categorical traits were selected for invertebrates (Table 3.1). For each trait, each taxon (e.g. species) within the associated trophic level was assigned a single trait value/category where possible, based on information in the literature (see ‘Data Availability’ section). Categorical trait information was combined with abundance data collected from pitfall and pan traps, or quadrat cover for plants, such that the trait dataset comprised the number of specimens (or percentage cover for plants) belonging to each trait category for each sample. This allowed for comparisons with the abundances of taxonomic identities. Continuous traits (in plants) were represented by community weighted means of scaled and centred trait values using the 'scale' R function, following log-transformation where appropriate.

Table 3.1. Traits used in the analysis of effect of farming system (agroforestry alleys versus arable) on community trait responses for three trophic levels. Within each trait, each taxon (e.g. species) was assigned a single trait value/category where possible.

Trophic level	Trait	Trait values / categories
Plants	Perenniality	Annual / biennial, perennial
	Clonality	Creeping, non-creeping, part-creeping
	Cotyledons	Monocot, dicot
	Month of first flowering	Month as a continuous variable
	Flowering duration	Number of months (continuous variable)
	Seed mass (g 1000 seed weight)	Continuous variable
	Height (cm)	Continuous variable
	Specific leaf area (SLA, mm^2/mg)	Continuous variable
Herbivorous invertebrates	Need for year-round vegetation	No requirement for year-round vegetation, some requirement, need for year-round vegetation
Herbivorous and natural enemy invertebrates	Diet of functional life-stage	Generalist (consumes multiple taxonomic orders), granivore, specialist (preferred prey limited to one or two taxonomic orders)
	Domain of functional life-stage	Broad (regularly hunts at ground level and higher on plant stems or aerially), base of plant or ground, foliar or aerial, within plant (herbivores only)
	Wings	Winged, part-winged (e.g. only some life-stages winged or dimorphic), unwinged
	Overwinter life stage (OW)	Egg, immature, adult, multiple
	Lifecycle	No pupal stage (exopterygote), pupal stage (endopterygote)
Natural enemy invertebrates	Hunting strategy	Active, ambush-and-pursue or sit-and-wait

A partial redundancy analysis (pRDA) was run separately for taxonomic and trait data, for each of the three trophic levels. For invertebrates, separate taxonomic pRDAs were run using (i) order-level resolution (or class/sub-class for some non-insect invertebrates such as millipedes, see Appendix 5) and (ii) the most precise taxonomic resolution in the dataset. This led to eight pRDAs. This method was chosen as pRDA allows multiple response and explanatory variables, while covariables can be ‘partialled out’, i.e. their effects removed before the RDA is calculated. Taxa or traits were the response variables, farming system (agroforestry or arable) was the single explanatory variable, and site and month/year were ‘partialled-out’ covariables. We also ran (i) trait pRDAs for herbivores and natural enemies using month/year (as a factor) as the single explanatory variable, separately for each farming system (agroforestry versus arable system), to explore the effect of seasonality on traits in each farming system, and (ii) pRDAs in the agroforestry system only for invertebrates (because three sites were available), with distance from tree row as the single explanatory variable, to explore spatial effects. All response variables were chord-transformed to account for the high proportion of zeros (Legendre & Gallagher 2001). For plant pRDAs, the analysis used data from the two organic sites but not the conventional site, due to low non-crop plant cover at the latter site, probably because of herbicide use.

To compare the performance of trait and taxonomic pRDAs, adjusted R-squared values, F-statistic and p-values were calculated, based on 999 permutations. The analysis was undertaken using the R package ‘vegan’ (Oksanen et al. 2013).

Diversity metrics

Studies of agro-ecosystems traditionally measure taxonomic richness and Shannon diversity, but functional trait diversity is emerging as a more meaningful alternative (e.g. Greenop et al. 2018). Firstly, we calculated taxonomic richness and Shannon diversity for each of the three trophic levels, using ‘vegan’ (Oksanen et al. 2013). The analysis used the most precise resolution available in the dataset, including specimens identified to lower resolutions (e.g. order, family), because the effects of land use on order-level diversity and species diversity are similar in arthropods (Biaggini et al. 2007). We also calculated functional diversity of natural enemies based on effect traits that have been shown to play an important role in herbivore suppression (Greenop et al. 2018). These comprised hunting strategy, dietary specialism and habitat domain (Table 3.1). Each natural enemy taxon was assigned a category for each trait using information in the literature (see 'Data Availability' section).

Phylogenetic diversity can be combined with trait information to account for potentially important overlooked traits (de Bello et al. 2017). We therefore calculated phylogenetic diversity of natural enemies using a proxy phylogenetic tree based on the classification of each taxon, using the R package 'ape' (Paradis & Schliep 2018). As traits and phylogeny are often related and non-independent, the overlap in variation was decoupled using the 'decouple' R function (de Bello et al. 2017). This was used along with the 'melodic' function (de Bello et al. 2016) to calculate abundance-weighted Rao indices for functional diversity, phylogenetic diversity, and decoupled phylogenetic diversity. The latter represents the phylogenetic diversity of the natural enemy community, excluding the considered traits, and thus indicates potentially unexplored traits.

The effect of farming system (agroforestry alleys versus arable) on each diversity metric was analysed using mixed models in the 'lme4' package (Bates et al. 2015), where each richness or diversity metric was the response variable, farming system was a fixed effect and both site and month/year were random intercept effects. We also ran models (i) for individual sites, to test the influence of individual sites on the overall effects, (ii) with a fixed interaction effect between sampling month and farming system, with site as a random effect, to explore patterns in richness and diversity effects over the season, and (iii) for the agroforestry system only, with distance from tree row as the single explanatory variable, to explore spatial effects. Model assumptions were inspected using residual plots as recommended by Harrison et al. (2018).

Pest and weed suppression

The effect of farming system (agroforestry versus arable) on the abundances of eight key pest/weed taxa was analysed using generalized linear mixed models. Key pests were defined as those included within AHDB’s field crop pest encyclopaedia (AHDB 2015). Models were initially fitted with a Poisson link and inspected for overdispersion, following which a negative binomial link was fitted if necessary. Months and/or sites with very low counts were excluded from the analysis where necessary to improve model fit (Appendix 6). Farming system was the single fixed effect, with site and month/year included as random effects where they were represented by more than one level. For each response taxon, data was derived from the sampling method that had the highest capture rate for that taxon. Further information on model selection is provided in Appendix 6. We also ran models for individual sites, for those taxa analysed at more than one site, to test the influence of individual sites on the overall results. Spatial effects within the agroforestry system were explored by running models with distance from tree row as the single explanatory variable.

3.4 Results

3.4.1 Responses of traits versus taxonomic-identities

A total of 80,186 specimens representing 183 taxonomic groups were collected from the pitfall traps, whilst pan traps yielded 313,132 specimens from 172 taxonomic groups. Farming system (agroforestry crop alleys versus arable) was a better predictor of trait than taxonomic composition for all three trophic levels, according to pRDAs (Fig. 3.1). Improved taxonomic resolution improved predictions for natural enemies and herbivores (Fig. 3.1).

The taxonomic pRDAs suggested idiosyncratic responses of taxa to farming system, for example two herbivorous fly (Diptera) families strongly contrasted in their response (Fig. 3.2c). Of the natural enemy taxa, wolf spiders (Lycosidae) were most strongly associated with the agroforestry alleys. Ground beetles (Carabidae) showed contrasting responses, for example, *Harpalus rufipes* was strongly associated with the agroforestry alleys, whilst *Anchomenus dorsalis* was associated with the arable control fields (Fig. 3.2e).

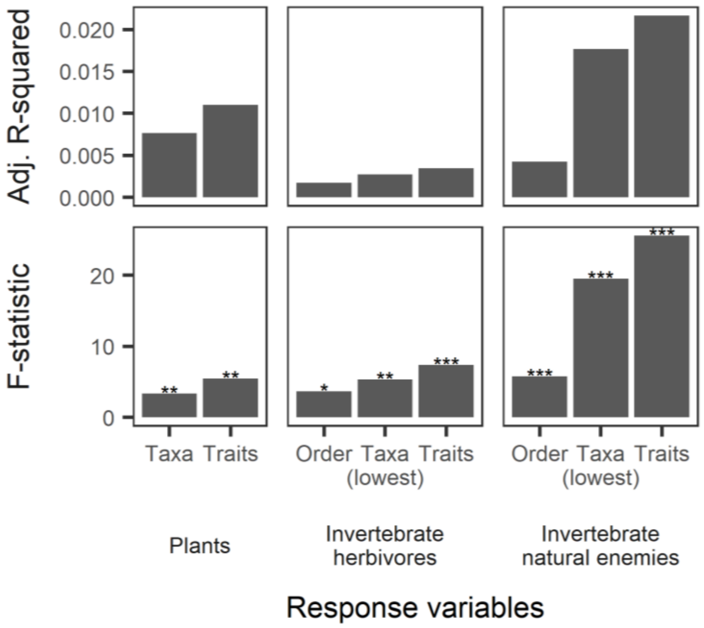

Figure 3.1. Comparison of pRDA performance, where taxa or traits were the response variables for each trophic level (i.e. each x-axis label represents a separate pRDA). The single explanatory variable in all pRDAs was farming system (agroforestry alleys versus arable). Adjusted R-squared values represent the explanatory power of the models, whilst F-statistics represent the significance of the models based on 999 permutations. Asterisks represent p-values (***<0.001, **<0.01, *<0.05, †<0.10).

Plant traits that were more associated with the agroforestry alleys than the arable control fields included late flowering season, short flowering duration, perenniality, and creeping habit (Fig. 3.2b). For herbivorous invertebrates, the need for perennial vegetation in the lifecycle, specialist diet, part-winged (e.g. dimorphic) and lack of pupal stage were positively associated with the agroforestry alleys (Fig. 3.2d). Similarly, natural enemy traits for granivorous or specialist diet, lack of wings and lack of pupal stage were more associated with agroforestry alleys than arable fields (Fig. 3.2f). However, the effect of farming system on overwintering life-stage and habitat domain contrasted between trophic levels. Seasonal patterns in trait profiles were similar between farming systems (Appendix 8). There were no apparent spatial effects within the agroforestry alleys on invertebrate taxa or traits (Appendix 9).

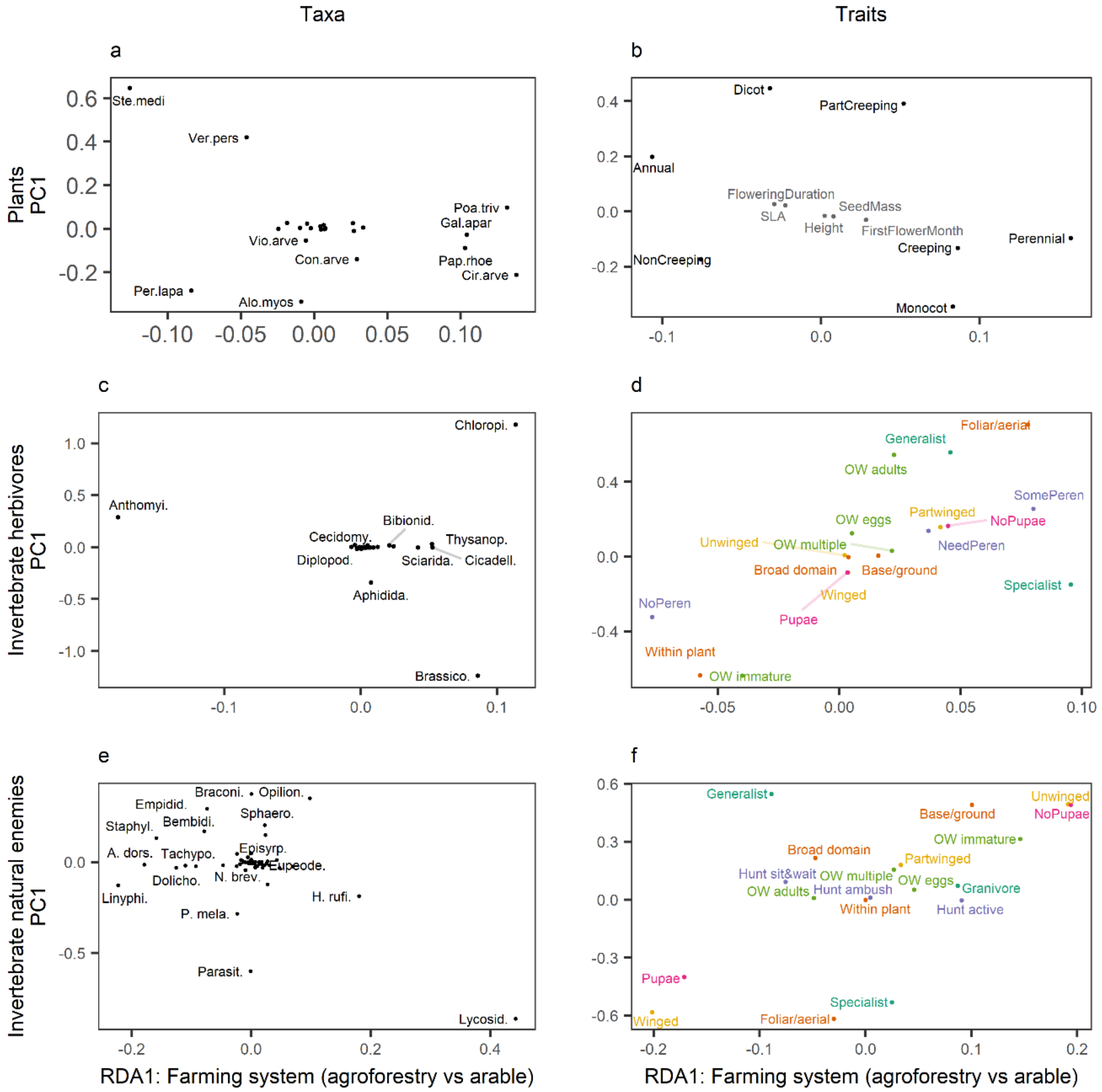

Figure 3.2. Partial redundancy analysis of taxa and traits (each column), for each of three trophic levels (rows). Farming system (agroforestry alleys versus arable) was the single explanatory variable, therefore higher x-axis values represent stronger association with agroforestry alleys relative to the arable system. Site and month/year were ‘partialled out’ covariates. Trait labels correspond to Table 3.1. Grey labels in Figure 3.2b represent continuous traits, which are on a different scale to the categorical traits (in black). Labels in Figures 3.2d and 3.2f are colour coded by trait category. Only the most abundant taxa are labelled. See Appendix 7 for species’ abbreviations.

3.4.2 Effect of farming system on diversity metrics

Taxonomic richness and Shannon diversity were higher in the agroforestry alleys than the arable control fields for all trophic levels, but exhibited a ‘pyramid’ pattern with stronger, significant effects at lower trophic levels, and a non-significant response for natural enemies (Fig. 3.3). Phylogenetic diversity of natural enemies was also not significantly different between agroforestry alleys and arable fields, but functional diversity of natural enemy effect traits, based on dietary specialism, hunting strategy and habitat domain, was significantly higher in the agroforestry alleys than the arable fields (Fig. 3.4). Decoupled phylogenetic diversity was not significantly different between agroforestry alleys and arable fields, indicating that important trait information was not overlooked in the functional diversity metric (Fig. 3.4). There were few clear seasonal differences between farming systems, although Shannon and phylogenetic diversity of natural enemies was greater in the agroforestry alleys early in the season, relative to the arable fields (Appendix 10).

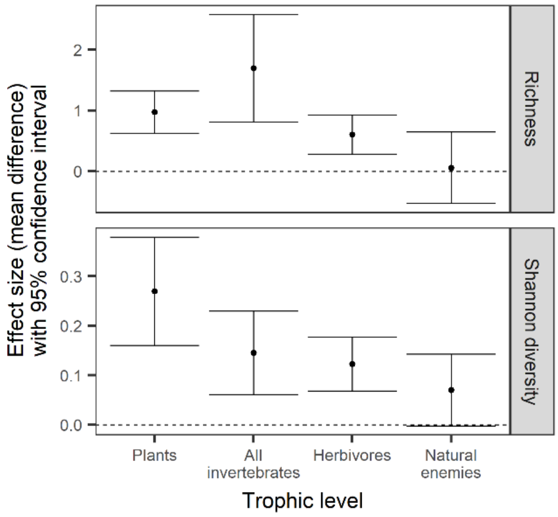

Figure 3.3. The effect of farming system (agroforestry alleys versus arable) on taxonomic richness and diversity for each trophic level, according to mixed model outputs where farming system was the single fixed effect, with site and month/year as random effects. The area above the dashed line represents higher values in the agroforestry alleys than the arable system. ‘All invertebrates’ represent herbivores, natural enemies and others e.g. detritivores. See Appendix 6 for further information.

The effects of farming system on diversity metrics were reasonably consistent at the site level. At all sites, Shannon diversity of plants, herbivores and pooled invertebrates was higher in the agroforestry alleys than the arable fields, while only one site showed a different response for taxonomic richness (Appendix 11). Similarly, functional diversity of natural enemies was higher at all three sites in the agroforestry alleys than the arable fields (Appendix 11). Within the agroforestry system, greater distance into the crop alleys slightly but significantly decreased Shannon diversity of herbivores, and taxonomic richness of pooled invertebrates, herbivores and plants (Appendix 9).

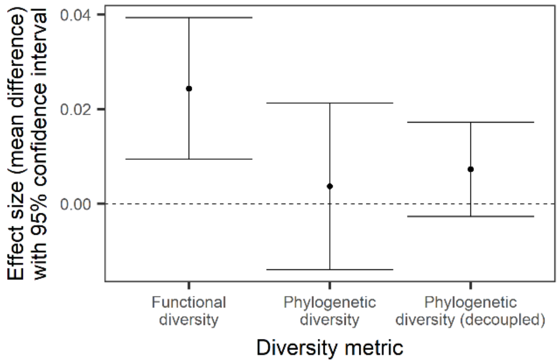

Figure 3.4. The effect of farming system (agroforestry alleys versus arable) on functional and phylogenetic diversity for natural enemies, based on mixed models as described at Figure 3.3. The area above the dashed line represents higher values in agroforestry alleys than the arable system. See Appendix 6 for further information.

3.4.3 Pest and weed suppression

The effect of farming system on the abundance of arable pests and weeds varied by taxon (Fig. 3.5). Three taxa were significantly suppressed in agroforestry compared to the arable fields. Of these, root flies (Diptera: Anthomyiidae) were consistently suppressed in the agroforestry system at all three sites (Appendix 11), with an overall reduction of 38%. A sub-sample of over 500 root flies was identified to species level; the dominant species was *Delia platura*, which represented over 90% of specimens at each site. Pollen beetles *Brassicogethes* spp. and wheat steam sawfly *Cephus pygmaeus* were also significantly suppressed in the agroforestry system, by 57% and 37% respectively, but could only be analysed at one site. A further three taxa, comprising grain aphid *Sitobion avenae* counts on wheat at one site, frit flies (Diptera: Chloropidae), and click beetles (Coleoptera: Elateridae), did not significantly differ in abundance between the agroforestry and arable systems, with different responses among sites (Appendix 11). Slug abundance was 39% higher in the agroforestry crop alleys than the arable fields, which was significant at both sites analysed. The effect of farming system on non-crop plant cover differed among the two sites in which plant cover was recorded (Appendix 11), but overall was 27% higher in the agroforestry alleys than arable fields. Spatial effects of pest abundance within the agroforestry fields were weak, with significant effects limited to an increase in wheat stem sawfly abundance with distance from tree row (Appendix 9).

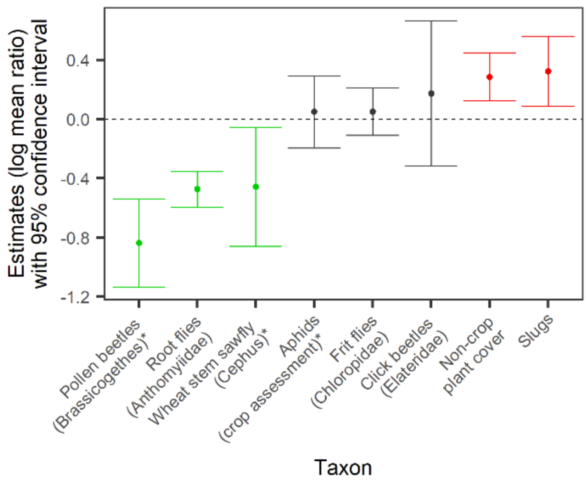

Figure 3.5. The effect of farming system (agroforestry versus arable) on the abundances of arable pests and coverage of weeds, derived from negative binomial generalized linear mixed models. The area above the dashed line represents higher abundance/cover in the agroforestry than the arable system. Taxa marked with an asterisk were only analysed at one site as they were either scarcely recorded at the other sites, or in the case of pollen beetles, are a pest of oilseed rape, which was only grown at one site during the study period. Further outputs are provided in Appendix 6.

3.5 Discussion

Trait profiles in the agroforestry crop alleys were significantly different to the arable fields at all three trophic levels, with improved model performance compared with taxonomic identities for all trophic levels. We also found greater taxonomic richness and Shannon diversity in the agroforestry crop alleys, relative to the arable control fields, with stronger effects at lower trophic levels. Significant effects on natural enemy diversity were only detected using functional trait analyses. The effect of farming system on pest/weed abundance differed by taxon, which suggests that pest control issues in agroforestry systems differ to those in arable systems.

3.5.1 Interpreting functional biodiversity using a trait-based approach

For plant traits, we found that perenniality, creeping habit, and late and brief flowering were more associated with the agroforestry alleys relative to the arable fields. Although replication for plant data was limited to the two organic sites, this finding is well supported by ecological theory. In particular, the CSR (Competitive, Stress tolerant, Ruderal) classification predicts that ruderal plant communities, characterised by short lifespan, rapid growth and flowering, and reliance on seed dispersal, are adapted to higher disturbance environments (Grime 1977). The plant community in agroforestry alleys is therefore less similar to a ruderal community and shows more characteristics that are expressed in competitive communities, reflecting the lower disturbance that occurs in these systems resulting from the presence of permanent vegetation strips.

For invertebrate communities, we found evidence of more diet-specialised herbivores and natural enemies in the agroforestry alleys relative to the arable fields. We hypothesise that this is because specialist invertebrates are more sensitive to local and landscape simplification than generalists (Gámez-Virués et al. 2015; Tscharntke et al. 2012), probably due to the lower dispersal ability and home ranges of specialists, although the strength of the effect varies according to scale (Chaplin-Kramer et al. 2011; Tscharntke et al. 2005). Granivorous natural enemies, which comprised carabid beetles such as *Harpalus* spp., were also more strongly associated with the agroforestry alleys than the arable fields, possibly because these carabids depend on local sources of seed food compared to predatory carabids (Woodcock et al. 2010).

Herbivorous invertebrates were more associated with the foliar domain in the agroforestry alleys, which could reflect the year-round availability of that domain in the agroforestry system, in contrast to the arable system. Natural enemies showed a different pattern, with the ground domain more associated with the agroforestry alleys, possibly explained by the more limited dispersal ability of ground-based predators. Exopterygotes (no pupal stage in the lifecycle) and partly- or unwinged traits were also associated with the agroforestry alleys for both trophic levels, which could be explained in terms of dispersal ability. Poor dispersers, such as those without wings, respond more strongly to localised beneficial conditions because they experience their environment at a smaller scale compared to more mobile invertebrates (Tscharntke et al. 2005, 2007).

Therefore, we propose that invertebrate trait responses to farming system can be explained in terms of reduced disturbance and the availability of year-round vegetation. This is supported by previous findings of carabid beetle community trait differences between tree rows and crop alleys in agroforestry systems during winter (Boinot et al. 2019b). Taxonomic responses were less informative in our results. For example, the responses of ground beetles to farming system varied widely among species, which has been observed in other diversified farming systems (Jowett et al. 2019; Li et al. 2018; Varchola & Dunn 2001), probably because of the diversity of functional traits within this family.

The trait-based approach also had methodological advantages over a taxonomic-identity analysis. Multivariate pRDAs based on traits as response variables improved the variance explained by farming system, suggesting that this approach can detect a stronger signal with less noise than a taxonomic-identity approach. Therefore, the trait-based approach has potential methodological advantages in the study of agro-ecosystems and can improve the generality and mechanistic understanding of findings.

3.5.2 Diversity metrics: functional, taxonomic and phylogenetic

Our finding of higher taxonomic richness and diversity in the agroforestry alleys compared with the arable fields is supported by previous findings in agricultural systems which have a lower management intensity (Attwood et al. 2008; Lichtenberg et al. 2017). We also found a stronger benefit to natural enemy Shannon and phylogenetic diversity early in the season, which suggests that agroforestry could play an important role for overwintering natural enemies. This is supported by the results of a previous study that investigated carabid beetles in an agroforestry system in France (Boinot et al. 2019b). We found weak but statistically significant spatial patterns in the agroforestry system, which suggests that the tree rows were driving the increased richness and diversity, but have far-reaching effects into the crop alleys.

Taxonomic diversity effect sizes decreased with increasing trophic level, which could be explained by the differing scales at which each trophic level experiences the surrounding landscape. Lower trophic levels are predicted to have smaller home ranges and dispersal ability and are therefore more influenced by local patch quality than landscape composition (Tscharntke et al. 2005). As such, the promotion of agroforestry systems to increase the biodiversity of higher trophic levels may only be achieved at large spatial scales.

Despite the lack of significant effects on Shannon diversity or phylogenetic diversity for natural enemies, functional trait diversity was significantly higher in the agroforestry crop alleys than the arable control fields. According to a meta-analysis of mesocosm studies, functional trait diversity of natural enemies is a stronger predictor of prey suppression than metrics based on taxonomic-identity or phylogeny (Greenop et al. 2018). We would therefore recommend that consideration is given to the calculation of this metric in future studies of conservation biological control.

3.5.3 Pest suppression

The effect of farming system on pests and their natural enemies varied among taxa. For example, root flies were strongly suppressed in the agroforestry system at all three sites, but slugs were 39% more abundant in the agroforestry alleys than the arable fields, with a consistent effect across the two sites analysed. Similar taxon-dependency has been observed in responses to flower margins (Eggenschwiler et al. 2013; Tschumi et al. 2015). This highlights the limitations of attempting to infer pest control service by studying a single taxon, such as aphids, while crop rotation is also likely to be an important factor.

The natural enemy assemblages of each specific pest taxon can be expected to have many commonalities, particularly generalist predators such as spiders and many species of carabid and rove beetle. Therefore, the contrasting responses of pest taxa to farming system suggest that bottom-up habitat effects could drive pest suppression to a greater degree than top-down predation or parasitism.

Although the replications of pest taxa and sites in this study were inevitably limited, we hypothesise that pest suppression effects can be explained in terms of response traits, particularly resource attraction, mobility, and sensitivity to disturbance. For example, adult root flies and pollen beetles are highly mobile and attracted to freshly disturbed soil and flowers respectively (AHDB 2015), both of which were more abundant in the arable than the agroforestry fields (for pollen beetles, when the arable crop was oilseed rape). Conversely, slugs are broad generalists, have limited mobility, and are sensitive to cultivation. Agroforestry systems provide year-round vegetation and refuges from cultivation, unlike arable systems, which could explain the greater abundance of slugs in agroforestry alleys than arable fields. This is a similar concept to the resource concentration hypothesis, which predicts that immigration of diet-specialist pests is higher, and emigration lower, in monocultures compared to polycultures (Root 1973). We therefore propose that agroforestry systems have different pest control issues than arable systems, based on the traits of those pests.

3.5.4 Caveats

Our approach was to rapidly characterise traits across plant and invertebrate communities, therefore some invertebrate traits could not be included in the analysis due to taxonomic resolution or a lack of literature. The study system is a rare, innovative design, which limited the availability of sites for replication. Nevertheless, all sites featured a pair of agroforestry and arable fields under identical management and in similar landscape contexts, whilst we sought to maximise within-site and temporal replication. The trait-based approach detected significant differences between farming systems and facilitated a mechanistic understanding of the effects, demonstrating the value of this approach even with limited replication among sites.

Site-level replication for plants and some pest taxa was further reduced because of the low coverage or abundance at some sites, which led to their exclusion from the analysis in some cases (Appendix 6). Therefore, further confirmation of the results, particularly for plants and invertebrate pest taxa, is recommended.

Previous studies have demonstrated benefits of grass and flower strips on natural enemy abundances and pest suppression (e.g. Collins et al. 2002; Hatt et al. 2017). As such, it is probable that the effects we find are primarily driven by the uncultivated strips of field-layer perennial vegetation rather than the trees themselves. Ideally, to disentangle the ecological effects of trees from uncultivated strips, this would be tested by comparing vegetation strips with and without trees. Nevertheless, the presence of productive trees provides an economic justification for a high density of ground vegetation strips within a field, compared to what would likely be tolerated by farm managers with treeless vegetation strips. Therefore, from an applied perspective it is most appropriate to consider trees and ground vegetation strips in combination. At our study sites, the tree rows occupy approximately 10% of the agroforestry fields, which is far greater than typical densities of non-productive strips. For example, the recommended density of beetle banks in the UK is one per 16 ha field (Royal Society for the Protection of Birds 2017). In addition, the presence of trees is likely to increase the longevity of the permanent vegetation strips, because they offer a financial incentive for retention for the duration of their productivity.

The farms in our study were all ecologically managed to some extent. For example, at two of the three sites, arable field sizes were relatively small (c. 6 ha or less, Appendix 3) and set within well-wooded landscapes. Therefore, biodiversity could be expected to be relatively high, which could have masked effects relative to what would be expected from more intensively managed farms in simpler landscapes (Fahrig et al. 2015; Jonsson et al. 2015; Staton et al. 2019; Tscharntke et al. 2005). Furthermore, the agroforestry systems we studied were relatively recently established, which might have limited the colonisation of new species compared to more established systems (Staton et al. 2019). Therefore, longer established systems in intensive landscapes could potentially achieve greater effects than we found in this study.

Comparisons between functional, taxonomic and phylogenetic diversity have been described as ‘conceptually flawed’ on the basis that the latter two do not take traits into account, and therefore do not use comparable information (Mlambo 2014). We consider there is merit in making such a comparison, but careful interpretation is required. Our findings do not necessarily mean that taxonomic and functional traits are fundamentally different, as we do not account for taxonomic traits. Instead, we show that more consistent and statistically significant patterns in the data can be detected by functional trait diversity rather than traditional taxonomic diversity metrics, such as Shannon diversity.

3.5.5 Conclusions

Our application of a trait-based approach to investigate the effect of farming system on functional biodiversity provided valuable insight into potential mechanisms behind the effects, which were consistent with reduced disturbance and the availability of year-round in-field vegetation in the agroforestry system. We found significantly higher functional trait diversity of natural enemies in agroforestry alleys versus arable fields, but this was not detected by taxonomic diversity metrics. The taxon-dependent effects of farming system on pest abundance demonstrates the need to consider multiple taxa in studies of agricultural diversification on natural pest control. These effects were more easily explained by response traits rather than top-down control by natural enemies. This suggests that the effect of farming system on weeds and invertebrate pests could be predicted at any individual farm, i.e. annual, disturbance-tolerant weeds and specialist, highly mobile pests are predicted to be suppressed in agroforestry systems, in contrast to perennial weeds and generalist, low-mobility pests. We recommend validation and further application of trait-based approaches in future studies of agroforestry and other diversified farming systems.

3.6 Data availability

Trait databases for invertebrates and plants are openly available within the supplementary data files at https://doi.org/10.1002/eap.2294. The raw taxonomic abundance data are available from the Dryad Digital Repository at https://doi.org/10.5061/dryad.rn8pk0p84.

4. Niche complementarity drives increases in pollinator functional diversity in agroforestry systems

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Author contributions:

Joint first-authored by TS and RW. Conceptualisation: all authors; study design: all authors; data collection: TS; formal analysis: TS with input from RW; investigation: TS; data curation: TS; writing – original draft preparation: TS and RW; writing – review and editing: all authors; visualisation: TS and RW; supervision: RG; project administration: TS.

In this chapter, we extend the trait-based approach in the previous chapter to reveal the effect of agroforestry systems, relative to arable controls, on pollinator communities by exploring trait distributions such as functional diversity rather than solely directional trait responses. This allowed us to reveal new mechanistic insights into community differences between farming systems.

4.1 Abstract

Diversified farming systems can benefit biodiversity, but it is less clear whether additional species play a redundant or auxiliary role in ecosystem functioning. Here, we collected pollinator and plant community data from three diversified agroforestry systems with paired monoculture arable controls to investigate the impact of additional species on functional diversity. For bees but not hoverflies, functional richness and dispersion were significantly higher in the agroforestry systems, and increased with system age, indicating elevated ecosystem functioning. Additional pollinator species in agroforestry systems supplemented

functional diversity through niche complementarity, especially for traits closely connected to the distribution and abundance of flowering plants. Nationally rarer species contributed substantially to functional richness but less so to functional dispersion, suggesting their contribution to landscape-scale pollination may be limited to maintaining gamma diversity. These mechanistic insights help explain why biodiversity and ecosystem functioning can depend on agroforestry system management.

4.2 Introduction

Sustainable intensification and the diversification of farming systems are suggested as possible solutions to global food security (Mbow et al., 2018.; Charles et al., 2014) and the biodiversity crisis (IPBES 2018; Lichtenberg et al. 2017), and as a way to increase resilience to predicted climate change (Gil et al. 2017; Kremen & Miles 2012). Agroforestry is one such example of a diversified farming system, and is defined as “the intentional integration of trees or shrubs with crop and animal production to create environmental, economic, and social benefits” (United States Department of Agriculture 2019). However whilst promising conceptually, few studies have systemically investigated these benefits and the scant evidence that is available is often equivocal, particularly with respect to the effects of agroforestry systems on functional biodiversity (Pumariño et al. 2015; Staton et al. 2019; Torralba et al. 2016). To some degree, this can be explained by how biodiversity is measured, for example in terms of the taxonomic scope and over what spatial and temporal scales (Boinot et al. 2019b; Griffiths et al. 1998; Staton et al. 2021b), and also the management of the agroforestry system (Boinot et al. 2020; Staton et al. 2021a). With appropriate management, agroforestry systems can increase biodiversity (Staton et al. 2021b; Torralba et al. 2016; Udawatta et al. 2019), although whether this enhanced biodiversity contributes to ecosystem functioning and ecosystem services remains largely unknown (Blüthgen & Klein 2011; Gonzalez et al. 2020; Nicholson et al. 2020).

Communities tend to be dominated by a few common species, which make up the bulk of the individuals, biomass and energy in an ecosystem (Gaston and Fuller, 2008; Gaston, 2011). Most species could therefore be considered 'rare', raising questions about their functional importance (Gaston 2012) beyond their intrinsic value (Soulé 1985). However, since 'rare' species are often specialists they can also be locally abundant (Gaston 1994), with a disproportionate influence on functional richness and a potentially important role in maintaining the integrity of ecological processes (Leitão et al. 2016). For example, in the case of plant-pollinator networks, the quality of pollination provided by specialist pollinators moderates the influence of intra-specific versus inter-specific competition at the landscape scale, which in turn promotes the coexistence of plants (Bergamo et al. 2020). In the case of crop pollination, regionally rare species can be locally important crop pollinators (Hutchinson et al. 2021; MacLeod et al. 2020; Vasiliev & Greenwood 2020), although they may have a limited role at individual sites (Kleijn et al. 2015; Nicholson et al. 2020). Understanding how rare species contribute to functional diversity could help to reveal the role rare species may play in supporting ecosystem function, stability and services.

An ambiguous link between biodiversity and ecosystem functioning can occur because the additional species in the more biodiverse system are either low in abundance (Gaston 2012) or they have similar traits to others, thereby limiting their contribution to the breadth of the community functional niche (Blüthgen & Klein 2011). By quantifying trait dimensions of species, it is possible to reveal whether the addition of species simply contributes to the redundancy and stability of an ecosystem function/service, or potentially improves it through a change in functional identity (Fig. 4.1, scenario 1) (Garibaldi et al. 2015), greater niche complementarity (Fig. 4.1, scenarios 2 or 3) (Martins et al. 2015; Woodcock et al. 2019) or functional evenness through a balancing of species' abundance in trait space (Fig. 4.1, scenario 4) (Villéger et al. 2008).

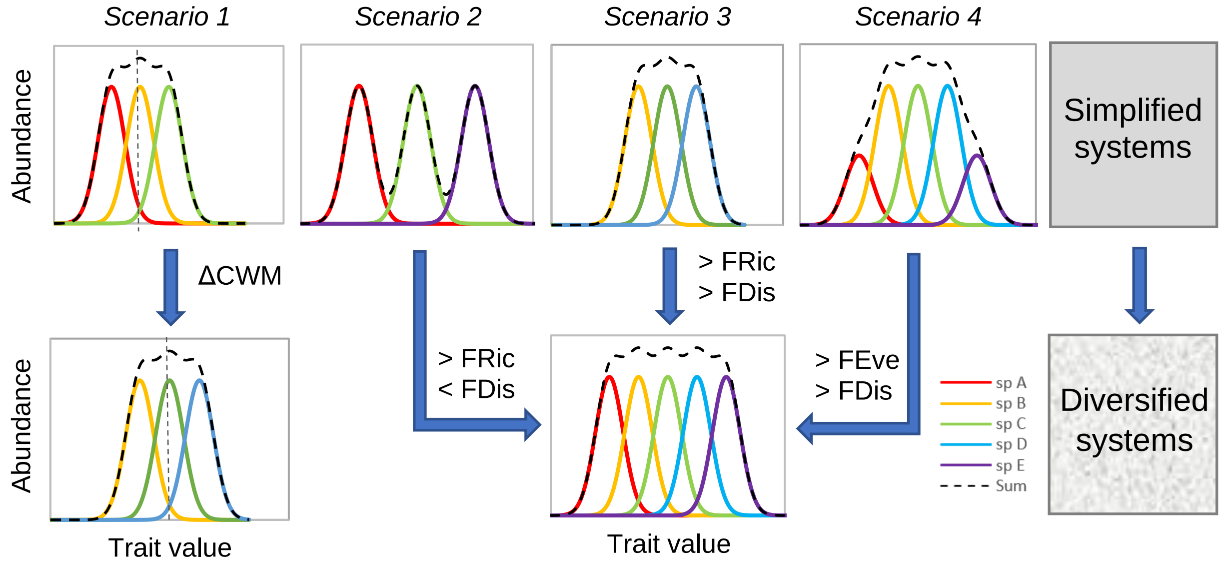

Figure 4.1. Higher levels of biodiversity and ecosystem function evident in more diversified systems may be attributable to functional community changes, including functional identity represented by a directional change in community-weighted mean traits (CWM; horizontal dashed line, scenario 1), and/or niche complementary represented by functional richness (FRic; scenarios 2 and 3), functional dispersion (FDis; scenarios 3 and 4), and functional evenness (FEve; scenario 4). Operators (e.g. < or >) represent the change in metric moving from the simplified to the diversified system. Response to a single trait value shown for illustrative purposes only.

Functional traits can provide insight into the mechanism of ecosystem function (Gagic et al. 2015; Wong et al. 2019). For example, bee tongue length is closely matched to floral nectar tube depth, which determines foraging efficiency (Klumpers et al. 2019). Bee wing or body size is correlated with foraging distance from nest sites (Greenleaf et al. 2007; Westphal et al. 2006) and manoeuvrability in complex environments (Ravi et al. 2020), therefore, this trait could be linked to spatial proximity of nesting and foraging habitats and vegetation structure. Pollinators also exhibit variation in the duration of their flight seasons, which has been linked to synchrony of floral resources (Duchenne et al. 2020; De Palma et al. 2015). Despite this potential for trait-based analyses to improve our mechanistic understanding of pollinator community responses to habitat complexity, previous findings have been inconsistent (Bartomeus et al. 2018; Coutinho et al. 2018; De Palma et al. 2015) and strongly differ according to which traits are included in the model (Kremen & M’Gonigle 2015). This limitation could be explained by the sole focus on directional trait responses (i.e. functional identity) rather than a consideration of functional trait diversity and niche complementarity (Wong et al. 2019).

In this study, we compare functional identity and diversity of bee and hoverfly communities in a diversified agroforestry system versus a simple arable monoculture system. To investigate the role of species niche complementarity we attribute differences in diversity to functional richness, evenness and dispersion metrics and quantify the explicit contribution of rarer species (at the national scale) to these metrics. Finally, we evaluate how differences in functional diversity, attributable to pollinator traits, relate to differences in floral structural diversity.

4.3 Methods

4.3.1 Field sites

The study sites comprised three working farms in eastern England, each with a paired agroforestry field and an arable control field under the same management and crop rotation. This paired field approach allowed us to control for confounding factors, such as surrounding landscape composition, soil type, farm management, and climate, as much as possible. Two of the study farms were organically managed, the third was conventional but applied the principles of Integrated Farm Management, including minimised pesticide use. Each of the agroforestry fields comprised an alley-cropping configuration, with single 3-4 m wide rows of trees (mostly apples) intercropped with 24 m wide arable crop alleys, containing wheat, oats, or oilseed rape (the latter was grown at one site, for one of the study years). The three agroforestry systems varied in their age since establishment, with the trees between four and nine years old at the time of sampling. A flower mix was sown under the trees at the time of tree planting (see Appendix 12 for species lists), which was cut up to twice per year during the study period. Further information on sites, including crop rotations, is provided in Appendix 3.

4.3.2 Experimental design

Data were collected as part of a wider study into the impact of agroforestry systems on biodiversity (Staton et al. 2021b). Wild pollinator species richness and abundance was quantified using pan traps over nine sampling visits across two active seasons (April to October, 2018 to 2019) at each of the three study sites. At the end of sampling, pan trap samples were passed through a 1 mm sieve with the contents transferred to specimen tubes and stored in a freezer. All bees and hoverflies were identified to species, and sex for bees, using an optical microscope and identification keys (Falk 2017; Stubbs & Falk 2002). Specimens of *Bombus lucorum* and *B. terrestris* were grouped because they could not be reliably separated. Following the approach of a previous study of pollinators in UK agroforestry systems (Varah et al. 2020), our analysis focussed on wild bees and hoverflies rather than honeybees *Apis mellifera*, whose abundance across sample locations could be biased by proximity to managed hives. Pollinators were also recorded using transect walks, with the data solely used for abundance analysis (Appendix 13) because specimens were identified to a broader taxonomic level (hoverfly, solitary bee, bumblebee, honeybee).

All sampling was undertaken at least 30 m from the nearest field boundary. Data from each sample location was pooled for each year, because of the high frequency of zeros in the original dataset. The first pan trap sample month (May 2018) was omitted from all analysis, because of the high number of missing samples (11 of 96). This month accounted for 0.8 % of all pan trap specimens. Nine sample locations with missing data (due to disturbed pan traps) were omitted from the analysis. Further details on the protocols for collection and identification of species can be found in Appendix 4.

4.3.3 Analysis

Trait selection

Pollinator traits were selected based on their demonstrated or hypothesised relationship to farming system and management. Trait values were assigned to each species based on a search of the literature and pre-existing databases, focussing on UK sources where possible (Appendix 14). Hoverfly traits were primarily sourced from the ‘Syrph The Net’ database (Speight et al. 2020) used in previous studies (Moquet et al. 2018; Schweiger et al. 2007). Hoverfly proboscis length was also considered but values depended on the method of measurement and could not be sourced for some species. Bee life-history traits were primarily sourced from Falk (2017), with tongue length imputed based on family and intertegular distance (Cariveau et al. 2016). Wing length was chosen over other size metrics such as body size or intertegular distance because sex-specific data for wing length was available for all species in our dataset. Bees were separated by sex within the analysis, i.e. males, females, and queens were treated as separate ‘species’, because many species exhibit wing length dimorphism. Nesting placement, brood parasitism, and diet breadth (oligolectic or polylectic) of bees were also considered but the species in our dataset lacked sufficient variation in these traits and so they were excluded from analyses.

Functional identity

All analysis was undertaken using R version 3.5.3 (R Core Team 2018). We used generalised linear latent variable models (GLLVMs) to investigate the association of functional traits with farming system and proximity to agroforestry tree rows. GLLVM is a model-based ordination approach which extends the generalised linear model to multivariate data, and offers improved modelling and verification of the mean-variance relationship compared with classical ordination methods such as non-metric multidimensional scaling (Hui et al. 2015; Niku et al. 2019a). We used a ‘fourth-corner’ GLLVM to test the interaction between traits and farming system or proximity to tree rows. Fourth corner analysis combines three known ‘corners’, comprising matrices of environmental data (in this case farming system or proximity to tree row) across sample locations, species abundance data, and species trait data, to infer the fourth corner, a matrix of trait-environment interactions (Brown et al. 2014).

Using the ‘gllvm’ R package (Niku et al. 2019b), separate GLLVMs were built for bees and hoverflies, and for the environmental variables ‘farming system’ (agroforestry or arable) and ‘proximity to tree row’ (distance from the centre of the 24 m wide alley), while site was an additional environmental variable in all models. Therefore, four separate trait models were built, each of which included all the selected traits for the taxon (Appendix 14). Additional models were built for each individual site, to compare effects among sites. These multi-trait models accounted for the combined effects of all traits. In addition, to explore the association of individual bee traits with farming system in isolation, we built separate GLLVMs for each of the five bee traits (Appendix 14), with site as an environmental variable.

A Poisson distribution with two latent variables was chosen for the GLLVMs, except for hoverfly multi-trait models for farming system (Poisson, three latent variables) and proximity to tree row (negative binomial, one latent variable), based on corrected Akaike Information Criterion values and visual inspection of residual plots to verify model assumptions. Site was included as a random slope effect. To test the statistical significance of the models, we also fitted equivalent null models without traits (to compare trait models) and performed a likelihood ratio test using the ‘anova’ function.

Functional diversity

The ‘FD’ R package (Laliberté et al. 2015) was used to calculate three functional diversity metrics, separately for bees and hoverflies, at each sample location; (i) functional richness, (ii) functional evenness, and (iii) functional dispersion (illustrated at Fig. 4.1) (Laliberte & Legendre 2010; Schleuter et al. 2010). Functional richness represents the volume of the trait space occupied collectively by the species present, a value which increases with species number but is independent of species abundance. Functional evenness is a measure of multi-dimensional trait variance, a value which is independent of species richness and increases with the levelling of species’ relative abundance and the even distribution of species in trait space. Functional dispersion is the mean distance of individual species to the centroid of all species in multi-dimensional trait space weighted by species’ relative abundance, a measure that is independent of species richness and arguably provides the best estimate of niche complementarity (Mason et al. 2013). Each metric was calculated by combining all traits for the taxon.

The effect of farming system on functional diversity metrics was tested using log(x+1) linear models for functional richness, binomial generalized linear models (GLMs) for functional evenness, and linear models for functional dispersion. Model assumptions were checked, including for overdispersion. For the bee models, the functional diversity metric was the response variable, and farming system and site were fixed interaction effects with main effect for farming system removed, to separately test the effect of farming system at each site. For hoverfly models, because there were no significant effects aside of functional richness at one site, results are presented for simple models with site as a random effect rather than an interaction.

Contribution of rare bee species

To define rare species, an occupancy dataset was sourced (Outhwaite et al. 2019), which reports occupancy in 1x1 km squares in the UK and occupancy trends for all bee species in our dataset. The occupancy dataset was produced by analysing observations from UK recording schemes in a Bayesian occupancy model to account for sampling biases. We defined rare species as those with an occupancy of less than 20% of 1x1 km cells in England in 2015 (the most recent year available), which accounts for 72% of bee species in England. This threshold of 20% allowed a reasonable number of species to be categorised as rare (15 of 39 species in our dataset), while there was a gap in the distribution of occupancies above 20% (the closest ‘non-rare’ species to the 20% threshold had an occupancy of 27.2%). We also considered categorising declining species, but only two species in our dataset were clearly declining in occupancy from 1970 to 2015 (confidence intervals not overlapping zero). Occupancy was not correlated with abundance in our dataset (Appendix 15).

The contribution of rare species to functional identity and each of the three functional diversity metrics (as described above) was investigated for bees by re-running the above analyses (individual trait models and linear models / GLMs for functional diversity) using a subset of the data excluding rare species, and comparing the results with the full dataset analyses.

Plant floral traits

Percentage cover of plants was recorded from a 1x1 m quadrat at each of the pan trap sample points in June 2018 and May 2019, and identified to species where possible. Plants in agroforestry tree rows were recorded along a 35 m length corresponding to the length of the adjacent sampling area, with coverage according to the DAFOR scale (see Appendix 12), which was then converted to approximate percentage (Dominant = 70%, Abundant = 37.5%, Frequent = 17.5%, Occasional = 6%, Rare = 1%). Each plant species was assigned to one of nine flower class traits based on nectar accessibility (Müller flower class), using the BiolFlor trait database within the ‘TR8’ R package (Bocci 2015; Klotz et al. 2002). These flower classes were ranked according to their nectar accessibility, and the proportion of plant cover corresponding to each flower class was plotted.

4.4 Results

A total of 2940 specimens of 71 wild pollinator species were collected in pan traps, comprising 1448 specimens of hoverflies (32 species) and 1492 specimens of wild bees (39 species). In accordance with previous studies, species richness and Shannon diversity of wild bees were significantly higher in agroforestry than arable systems, as was the abundance of wild pollinators on transects and in pan traps, but no such significant effects of farming system were found on hoverfly species richness and diversity (Appendix 13). A comparison between the GLLVM fourth corner multi-trait model and the null model further revealed that trait distributions differed between farming systems, for both bees and hoverflies (Fig. 4.2).

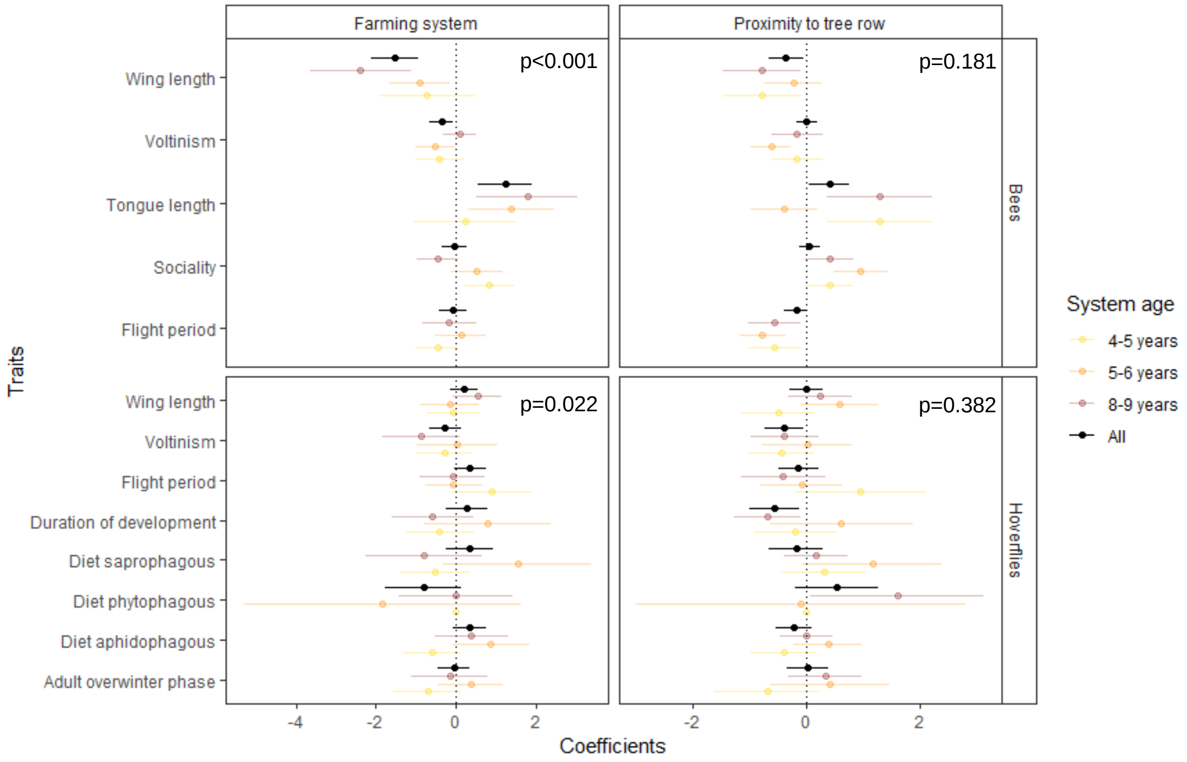

Figure 4.2. Estimated coefficients (points) and 95% confidence intervals (lines) for bee and hoverfly traits, according to GLLVM fourth-corner models using pan trap data. Points with x > 0 indicate that higher trait values are associated with agroforestry rather than arable systems (left column) or with tree row proximity (right column). Coefficients are modelled across the entire dataset using all traits, therefore coefficients for pooled sites can be different to individual sites. P-values are reported from likelihood ratio tests of fourth corner trait GLLVMs compared against null models without the trait interaction terms, with significant effects indicating that traits explain bee or hoverfly responses to farming system or tree row proximity. Each site contained one agroforestry and one arable system, therefore individual site-level results should be treated cautiously.

Trait coefficients derived from the GLLVM revealed that bee species sampled in agroforestry systems had shorter wing lengths and longer tongue lengths than those in adjacent arable systems, a finding that was consistently observed across all three sites (CIs not overlapping zero: Fig. 4.2). Univoltinism was also associated with agroforestry systems, although not consistently so among sites. The size of the effects for wing length and tongue length were found to increase with age of the three agroforestry systems and there was a congruous finding in space with respect to proximity to tree row within the agroforestry system (Fig. 4.2). Although the inclusion of traits was also a significant explanatory factor in the response of hoverflies to farming system, weak and inconsistent responses among sites obscured further interpretation of the role of life-history for this taxon (Fig. 4.2).

Repeating the modelling analysis for individual bee traits revealed further insights into the differences in trait distributions between these two farming systems. For instance, although it was confirmed that species in agroforestry systems have shorter wing lengths than those in adjacent arable systems, there was no longer a corresponding significant difference in tongue length and voltinism (Fig. 4.3). Instead, these trait distributions showed greater variance in agroforestry systems, which is evident in their measure of dispersion. Moreover, flight period and sociality, which were non-significant factors in the multi-trait analysis, were both significant, with longer flight periods and sociality associated with species recorded in agroforestry rather than arable systems, and appeared to be more dispersed (Fig. 4.3). The apparent generality of the emerging pattern of higher trait richness and dispersion of the bee community in agroforestry versus arable systems (Fig. 4.3) was confirmed by an analysis of pooled bee traits. The significance of farming system on functional dispersion increased with system age, while functional evenness followed a similar trend, but was not significant (Fig. 4.4). In contrast, farming system had no significant effect on hoverfly functional richness (t=1.168, p-value=0.246), evenness (t=0.538, p-value=0.591) or dispersion (t=0.152, p-value=0.880).

To evaluate the potential contribution of rare versus common species to ecosystem function, we compared the analyses above to equivalent analyses excluding rare species (see ‘Contribution of rare bee species’ for definition). The exclusion of rare species from single-trait GLLVMs increased the statistical significance of each model for three of the five traits (Fig. 4.3). Rare bee species were found to contribute to functional trait richness across all three sites, as expected given its strong correlation with species richness (Villéger et al. 2008), but only to functional evenness at two sites and functional dispersion at one site (Fig. 4.4). At the most established agroforestry system, where the effect of farming system on functional dispersion was strongest, the inclusion of rare species decreased the significance of functional dispersion, suggesting that the abundance of common species had a more important role. However at the second-most established system, rare species did contribute to the significance of functional dispersion, while at the most recently established system, rare species had no discernible effect, suggesting that these species did not occur in sufficient abundance to influence ecosystem function.

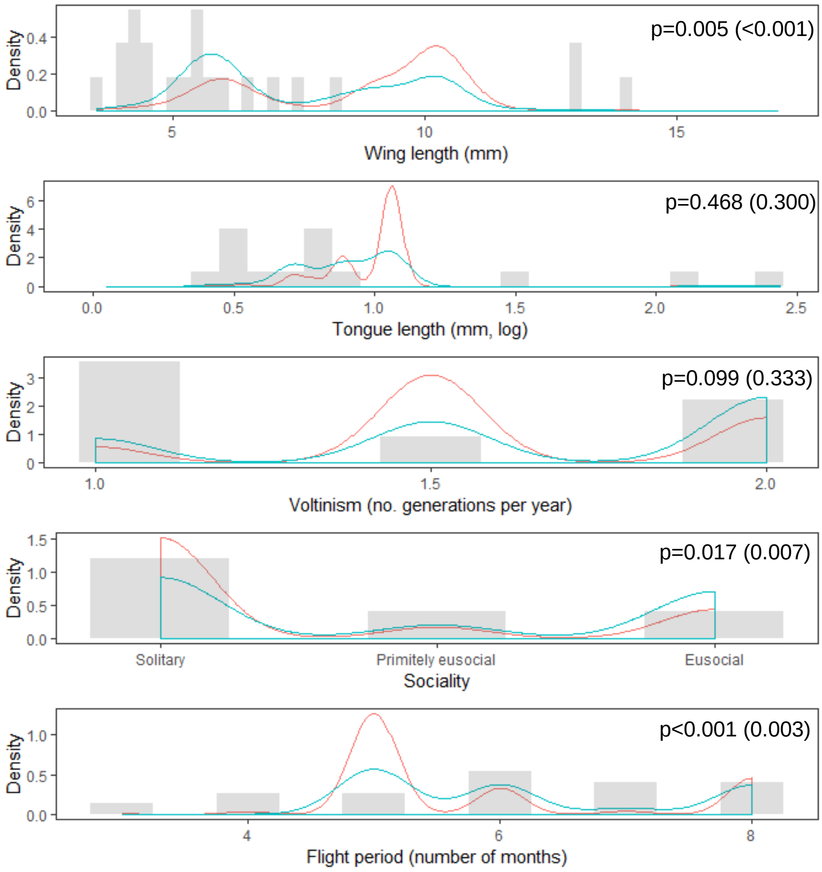

Figure 4.3. Density plots (smoothed histograms) of five bee traits in arable (red) and agroforestry (blue) systems, overlaid on density histograms showing the trait distributions of rare species (grey). For the wing length trait, species are separated into different sexes, hence there appear to be more rare species in this panel. P-values are reported from likelihood ratio tests of fourth corner trait GLLVMs compared against null models without the trait interaction terms, with significant effects indicating that the trait explains bee responses to farming system. P-values in brackets were calculated using a subset of the dataset without rare species. See Appendix 14 for trait definitions and coding.

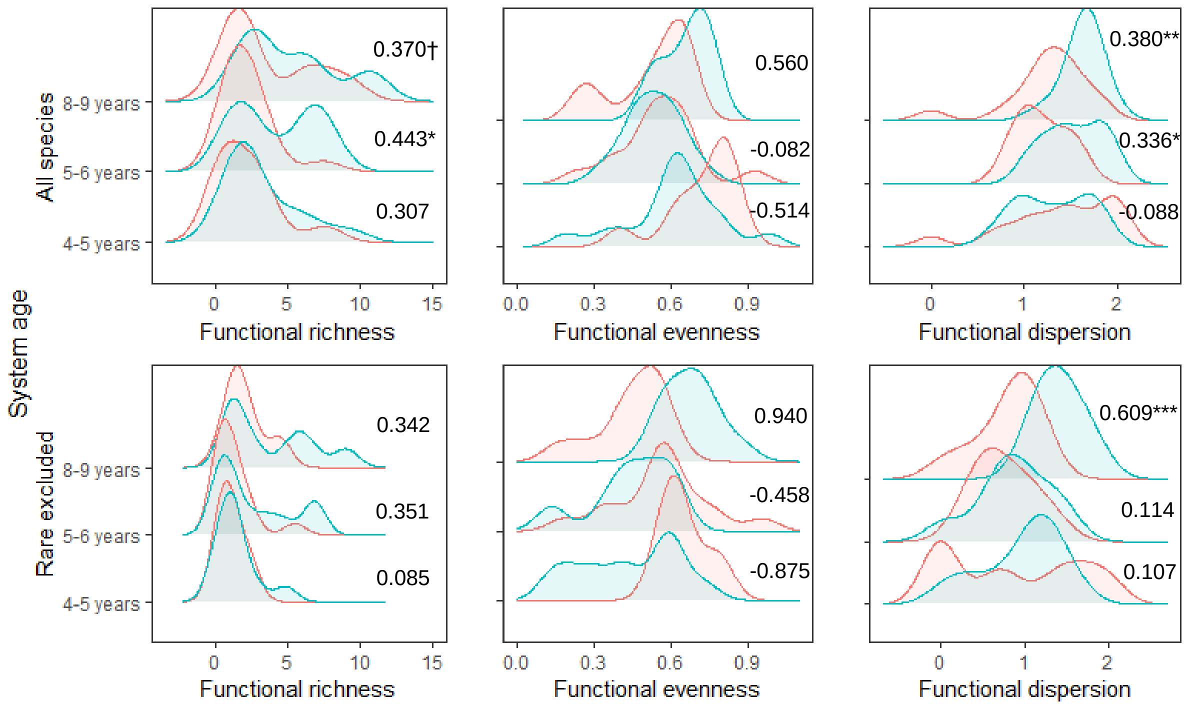

Figure 4.4. Density plots showing functional richness, evenness, and dispersion in agroforestry (blue) and arable (red) systems, calculated using all five bee traits, and separated by site. The top row represents all species, while the bottom row excludes rare species from the dataset (for both arable and agroforestry systems). Annotated numbers represent effect size taken from model coefficients, accompanied by significance based on p-values where *** < 0.001, ** < 0.01, * < 0.05, † < 0.1. Each level of system age was represented by two years of data from one site with paired agroforestry and arable systems.

To examine the potential causal role of plant traits on bee traits, namely greater variance in the trait distribution for tongue length, we evaluated the contribution of plant species diversity to dispersion of floral classes. We found a clear effect of greater richness and dispersion of floral classes in agroforestry systems, especially in or near tree rows (Fig. 4.5). Non-crop insect-pollinated plant cover in arable systems was primarily attributable to species with partly or totally hidden floral nectar, which are most suited to pollinators with intermediate tongue lengths. In contrast, flower structures of plant species in agroforestry tree rows were more diverse, including tubular flowers and flowers with open nectar, which are more favourable to pollinators with long and short tongues, respectively.

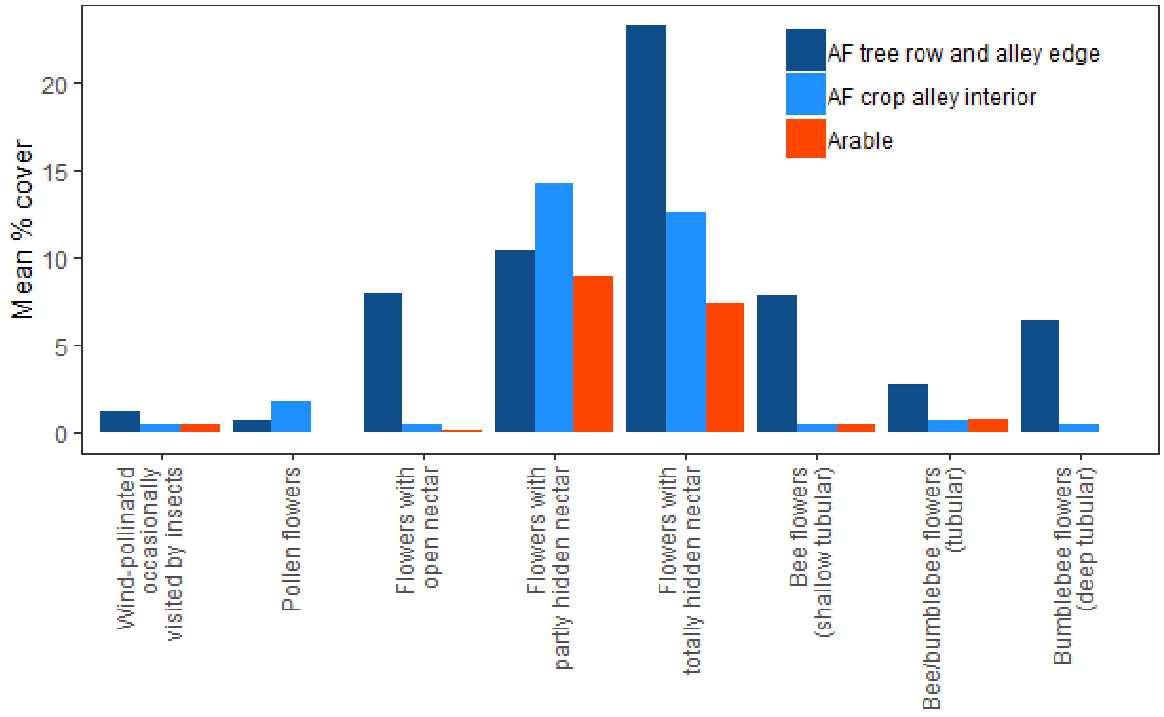

Figure 4.5. Percentage cover of non-crop plants according to flower classes, ordered by nectar accessibility (decreases along x-axis), in agroforestry (AF) tree rows and alley edges (0.5 m from tree row), crop alley interiors (5 and 9.5 m from tree row), and arable systems. Wind-pollinated plants are not shown.

4.5 Discussion

Pollinator abundance, and species richness and diversity of bees, were significantly higher in agroforestry systems than in arable systems, which is in agreement with previous findings (Varah et al. 2020). In addition, farming system modulated not only functional trait identities of pollinators, which has been the focus of previous studies and has led to inconsistent findings (Bartomeus et al. 2018), but also functional richness and dispersion in bees. These findings highlight the importance of niche complementarity for ecosystem functioning, and reveal mechanistic insights into bee community differences between farming systems.

Wing length, tongue length and voltinism of bees were all shown to significantly respond to farming system in the multi-trait model, with flight period and sociality also identified as significant factors when these traits were modelled separately. Of all the bee traits, wing length showed the clearest association to farming system, decreasing in response to agroforestry system and proximity to tree row within agroforestry fields, a relationship that was consistently observed across sites and significantly so in both the multi-trait and individual trait models. This single trait led to a change in the mean of the multi-trait distribution resulting in a change in the functional identity of the bee community, consistent with scenario 1 (Fig. 4.1). A shorter wing length could be advantageous at sites where there is a closer proximity of nesting and foraging resources or where greater flight manoeuvrability is needed to navigate the more cluttered vegetation structure (Greenleaf et al. 2007; Ravi et al. 2020; Westphal et al. 2006).

The multi-trait model also revealed that bees in agroforestry systems had longer tongue lengths, which is predicted to reflect an increase in the availability of flowers with a greater nectar tube depth (Klumpers et al. 2019). This association is independently supported here by our plant cover survey, which found a substantially higher proportion of tubular ‘bee’ flowers in agroforestry systems, particularly along tree rows. However, in contrast to the multi-trait model, the results of the single trait model revealed no such relationship – instead the bee community in the agroforestry system had larger variance in tongue length, with representation of both shorter and longer tongued species (consistent with scenario 3 in Fig. 4.1), which in turn reflected increases in plant cover for both open and tubular flowers. A similar pattern is seen for voltinism, in which the multi-trait model suggests bees in agroforestry systems have fewer generations per year on average while the single trait model instead reveals larger variance in voltinism, with greater representation of strictly univoltine and bivoltine species (consistent with scenario 4 in Fig. 4.1). This trait association may reflect corresponding changes in plant phenology and reduced disturbance during larval development in agroforestry systems (De Palma et al. 2015).

An extended flowering period and reduced risk of floral asynchrony could also explain why bees in the agroforestry system were more likely to be eusocial and have a longer flight period, at least in the single trait models. Social species typically have longer flight periods and generation times than solitary species, and have a faster response to resource provision (i.e.

flowers) through mass recruitment (Chapman & Bourke 2001; Persson et al. 2015). Social bees might therefore be better adapted to higher floral resource availability. Together, the observed changes in bee trait distributions are consistent with the predicted consequences of changes in floral and nesting resources in both space and time.

To better understand how these changes in bee species diversity and trait distributions impact ecosystem function, we examined the effects of farming system on various metrics of functional diversity (Blüthgen & Klein 2011; Gagic et al. 2015; Wong et al. 2019). Functional diversity of bees responded strongly to farming system in terms of functional richness and functional dispersion, but not functional evenness. Higher functional richness in agroforestry systems indicates that higher species richness increased niche complementarity rather than redundancy (Villéger et al. 2008), while the higher functional dispersion in agroforestry systems, which increased with system age, demonstrates that these additional species were sufficiently abundant to measurably contribute to ecosystem function. Further analysis revealed that rare species disproportionately contributed to functional richness in agroforestry systems but had little impact on functional dispersion at two out of three sites, which was probably due to their limited abundance. However, those offered refuge in agroforestry systems may still have a role in contributing to regional-level ecosystem functioning via their contribution to gamma diversity (Winfree et al. 2018) and promoting the resilience of pollination service to extreme climatic events (Brittain et al. 2013; Kühsel & Blüthgen 2015).

Although bee species richness, species diversity, functional richness, and functional dispersion were significantly higher in agroforestry than arable systems, there was no corresponding significant effect on hoverflies, reinforcing previous reports of differences between these two taxa in respect to their responses to land use and management (Meyer et al. 2009, 2017; Persson et al. 2020; Verboven et al. 2014). As central place foragers, bees are primarily constrained by the availability of nest sites in relation to floral resources, whereas the more mobile and diverse dietary requirements of hoverflies mean the response of this taxon to farming system may only be evident at larger spatial scales (Jauker et al. 2009; Power et al.

2016; Verboven et al. 2014). Although a previous study demonstrated hoverfly responses to land use and management at both the plot and landscape scale in relation to a similar suite of traits (Schweiger et al. 2007), we could find no such associations. However, since hoverflies are primarily short-tongued, relying on flowers with more accessible nectar (van Rijn & Wäckers 2016), the availability of flowering resources for adult hoverflies may not have been sufficiently different between farming systems because both are dominated by arable crops. Larval microhabitat and diet, two of the most important functional traits previously shown to determine species distribution in hoverflies (Schweiger et al. 2007), might also have not substantially differed between farming systems for the same reason, although the responses of the more numerous aphidophagous species may only be evident at the landscape-scale (Moquet et al. 2018). The lack of a definitive trait response to farming system in hoverflies stands in strong contrast to the significant and consistent trait associations evident for bees.

In addition to its ecological significance, our analysis of functional diversity of bees and their floral resources has implications for land-use management. Assuming that a) the increase in bee functional diversity in agroforestry systems is attributable to increases in plant diversity within the tree rows, and b) the spill-over of pollinators from habitat enhancements into crops can be limited (Nicholson et al. 2020), it might be expected that functional diversity benefits could be tightly associated with tree rows rather than increasing pollination service within the adjacent arable crop. However, although we did find that proximity to tree row structured bee communities in terms of functional identity, functional richness and dispersion were consistently higher across agroforestry crop alleys than in arable systems, indicating a spill-over effect from the tree rows into the adjacent crops. This suggests that agroforestry systems could enhance crop pollination service, which is supported by higher phytometer pollination levels in agroforestry systems than monocultures of arable or pasture (Varah et al. 2020). It also suggests that improvements in management of the tree row understorey to further promote floral diversity and to target specific crop pollinators, for example by favouring legumes for long-tongued bees, could further improve pollination services (Goulson et al. 2005; Hutchinson et al. 2021; Staton et al. 2021a).

In conclusion, our findings provide mechanistic insights into the benefits of agroforestry systems on biodiversity, ecosystem functioning and resilience. Community differences in bee traits reveal that higher species richness in these diversified farming systems can contribute not only to niche complementarity but also ecosystem function, as evidenced by higher functional richness and functional dispersion. These changes can be explained in terms of the spatial and temporal distribution of habitat resources, such as floral classes and nesting resources for bees, which could be optimised through appropriate management. In addition, diversified farming systems such as agroforestry can contribute to the conservation of rare species, which may contribute to ecosystem functioning at wider spatial and temporal scales.

4.6 Data availability

The data presented in this chapter will be made available upon publication of the associated manuscript.

5. Management to promote flowering understoreys benefits natural enemy diversity, aphid suppression and income in an agroforestry system

This chapter is derived from the following publication:

Staton, T., Walters, R., Smith, J., Breeze, T., Girling, R. (2021) Management to promote flowering understoreys benefits natural enemy diversity, aphid suppression and income in an agroforestry system. *Agronomy*, 11(4), 651. https://doi.org/10.3390/agronomy11040651

Author contributions:

Conceptualisation: all authors; study design: all authors; formal analysis: TS; investigation: TS; data curation: TS; writing – original draft preparation: TS; writing – review and editing: all authors; visualisation: TS; supervision: RG; project administration: TS.

The previous chapters identified differing effects of farming system (agroforestry versus arable) on functional biodiversity among sites, which could be explained by numerous site-dependent factors (as discussed in Section 2.5.3). This chapter evaluates the importance of one key confounding variable in isolation, namely management of the understorey vegetation below the trees.

5.1 Abstract

Agroforestry systems, where productive trees are integrated into agricultural land, can deliver benefits to biodiversity, natural pest control, and pollination, but the effects are highly variable. Recent advances in our understanding of flower strips in agricultural systems suggest that the management of the tree row understorey could be an important contributor to this variation. Here, we compare two cutting regimes for an understorey, originally seeded with the same flower mix, in the tree rows of an apple-arable agroforestry system: (i) uncut vegetation to promote a flowering understorey, and (ii) regularly mown vegetation. We recorded the effects of management on invertebrate pests, natural enemies, and pollinators, in both the apple and arable components. Apple trees above flowering understoreys supported significantly: (i) more natural enemies early in the season, (ii) fewer aphid colonies, (iii) fewer aphid-damaged fruits, and (iv) higher pollinator visitation, compared with those above mown understoreys. In the arable crop alleys, both taxonomic richness and Shannon diversity of ground-based natural enemies were significantly higher adjacent to flowering understoreys, compared with those adjacent to mown understoreys, early in the season. Financial modelling based on aphid damage to apples, mowing costs, and income from Countryside Stewardship grants, indicated that flowering understoreys increased farm income by £231.02 per ha of agroforestry compared with mown understoreys. Our results provide the first empirical evidence that management to promote flowering understoreys in agroforestry systems can be a win-win option to improve invertebrate diversity, associated ecosystem services, and farm income.

5.2 Introduction

The intensification of agricultural production, including habitat loss and the increased use of inputs such as pesticides, has been identified as a major cause of the global decline in invertebrate diversity (Sánchez-Bayo & Wyckhuys 2019; Wagner 2020). This loss of diversity can lead to a reduction in associated regulating ecosystem services, such as the natural regulation of agricultural pests through natural enemy (predator and parasitoid) activity, and insect pollination of agricultural crops (Deguines et al. 2014; Kremen et al. 2002; Rusch et al. 2016). This in turn can increase reliance on artificial inputs to maintain and improve food production in ways widely deemed to be environmentally damaging and unsustainable (Pretty 2008; Tilman et al. 2002). Sustainable intensification aims to reduce agriculture's dependence on external inputs by restoring natural processes and ecosystem services in tandem with improving agricultural productivity, for example, by integrating habitats for naturally-occurring pollinators and natural enemies within agricultural fields or landscapes (Pretty et al. 2018; Tittonell 2014). One such form of sustainable intensification is agroforestry, which is loosely defined as the deliberate incorporation of productive trees into livestock or arable farming systems (Gordon et al. 2018).

Agroforestry systems in arable settings (termed silvoarable systems) typically comprise an alley-cropping configuration in temperate regions, where single rows of trees are separated by alleys of combinable crops, usually between 12 and 50 m in width to allow for access by modern arable farm machinery. The integration of trees into arable fields can increase biodiversity and regulating ecosystem services, relative to monocultures (Smith et al. 2013a; Torralba et al. 2016; Tsonkova et al. 2012). In a meta-analysis of European agroforestry systems, Torralba et al. (2016) showed that overall biodiversity in all types of agroforestry systems was significantly higher than in monocultures of either agriculture or forestry, but was not significant for silvoarable systems. Furthermore, this positive effect in all agroforestry systems was not statistically significant for insect diversity. While other recent meta-analyses report that agroforestry systems decrease pest abundance and increase abundances of both pollinators and the natural enemies of pests, some individual studies find the opposite effect (Pumariño et al. 2015; Staton et al. 2019). As such, there is a need to improve our mechanistic understanding of the effects of agroforestry systems on functional biodiversity (Staton et al. 2019; Varah et al. 2020).

Ecological research on agroforestry systems has traditionally focussed on the biodiversity benefits of trees as providers of food sources, such as flowers, fruits, and organic matter, in addition to indirect benefits such as alternative prey/hosts and favourable microclimates for both soil and arboreal insects (Jose 2012; Tsonkova et al. 2012). In-field plant diversification is known to provide benefits to pollinators and predators of pests (Lichtenberg et al. 2017); therefore, management of the understorey beneath the trees that would promote plant diversity could contribute to invertebrate diversity by providing ground-level cover for overwintering, and additional food sources such as pollen and nectar (Boinot et al. 2019b; Staton et al. 2019). Recent research has demonstrated that incorporating flower strips into agricultural systems can benefit pollinators, natural enemies, and pest control services, although proximity to flower strip and age are important factors for pollinators (Albrecht et al. 2020; Ganser et al. 2020;

Gurr et al. 2017; Hatt et al. 2020). The incorporation of flower strips into tree row understoreys in silvoarable systems could provide even greater benefits, because the density of tree rows is typically higher than for flower strips which are usually restricted to field margins (Ganser et al. 2019).

Two previous studies have investigated the impact of understorey management on invertebrate natural enemies and/or pests in temperate silvoarable systems, by comparing vegetated understoreys with chemically weeded controls. In a study of three invertebrate taxa across three UK silvoarable systems, higher numbers of spiders and fewer slugs were captured in arable alleys adjacent to understoreys sown with a grass-clover mix than unvegetated understoreys, while the responses of carabid beetles varied according to species and site (Burgess et al. 2003). In a subsequent study in a silvoarable system in France, understoreys sown with a flower mix had no observable effect on grain aphid colonies or their natural enemies in the adjacent crop, although the flower mix did not establish as intended (Smits et al. 2012). However, there remains a lack of evidence for the effects of these various understorey management options on both biodiversity and, of more relevance to farmers, financial outputs (Kleijn et al. 2019). While flower mixes with infrequent cutting are often favoured by agroforestry farmers in the UK, on the presumption that this could provide habitat for beneficial insects in both the fruit and arable crops (Newman et al. 2018), intensive management of the understorey through regular mowing or chemical weeding has been recommended in alley-cropped silvoarable systems to restrict the spread of arable weeds (Reubens 2018).

Silvoarable systems with apple trees offer an ideal experimental system with which to evaluate the combined biodiversity and financial costs and benefits of understorey management. Apple trees are becoming a popular choice in new silvoarable systems particularly in the UK, and are suitable and viable options elsewhere in temperate regions (Gao et al. 2013), because of their potential to provide a quicker return on investment than timber, and limited shade impacts on the arable crop (Newman et al. 2018). Apples are also highly dependent on insect pollination

(Garratt et al. 2016a) and are susceptible to insect pest damage in the absence of pesticide application (Samnegård et al. 2019). In these silvoarable systems, it is common that a mixture of commercial and heritage apple varieties is grown, which are targeted at local specialised markets. For example, at the farm on which we conducted the current study, the apples are sold as a premium heritage juice product directly to the local public, which avoids any requirement to meet fruit appearance criteria that apply to eating and cooking apple markets.

In this study we sought to advance and broaden previous research of understorey management in agroforestry systems by considering management effects on invertebrate diversity, functional groups, resultant ecosystem service provision, and the financial costs and benefits, in both the tree and arable components of an apple-arable agroforestry system. We compare understoreys originally sown with the same flower mix but subject to two different cutting regimes, comprising management to promote flowering understoreys and frequently mown understoreys. We chose this approach rather than testing chemically weeded understoreys, because farmers typically value the environmental benefits of agroforestry systems and thus cutting is a more likely option in practice (García de Jalón et al. 2018; Graves et al. 2008). Specifically, our aims were to compare the effects of understorey management on (i) invertebrate pests, natural enemies, and pollinators in apple trees, in addition to fruit pest damage and pollination, and (ii) invertebrate diversity, pests, natural enemies, and yield, in the arable component. We also investigated seasonal patterns, where relevant. Finally, we aimed to predict the financial implications of understorey management, incorporating statistically significant findings of ecosystem service provision.

5.3 Methods

5.3.1 Study site

The study site comprised a silvoarable agroforestry system in Nottinghamshire, UK (0° 54' 38" W, 52° 59' 19" N). We selected the site because it: (i) is a working farm and therefore reflects real-world conditions, (ii) has established trees (planted in early 2014), (iii) is flexible in terms of management requirements and environmental stewardship agreements which allowed for the understorey to be experimentally manipulated, and (iv) contains distinct single species/variety tree blocks so that species/variety could be controlled within the experimental design. This silvoarable system occupied a 5.6 ha field. The trees were mostly apples *Malus domestica* on semi-dwarfing rootstocks arranged in single rows, each tree separated by 3 m within the rows, with a 3 m wide understorey. The apple trees are pruned annually but fruits were not thinned during the study year. The tree rows were seeded with a wildflower mix in 2014, which established well. The most frequent species comprised *Festuca rubra, Holcus lanatus, Deschampsia cespitosa, Leucanthemum vulgare, Picris echioides, Prunella vulgaris* and *Lotus corniculatus* (see Appendix 12 for plant species list). Prior to this study, the understorey was subject to infrequent mowing to promote flowering, typically comprising two late-season cuts. The arable alleys between the tree rows were 24 m wide, sown with barley during spring of the study year (2020). Other crops in the rotation included winter wheat (2019 harvest) and oilseed rape (2018 harvest). The soil texture is defined as a ‘slightly acid loamy and clayey soil with impeded drainage’ (Cranfield University 2020). The farm follows the principles of Integrated Farm Management, practising conservation tillage, minimising pesticide use in the arable component, and avoiding pesticide application to the apple trees.

5.3.2 Experimental design

Five experimental treatment blocks were selected within the site, each block containing one apple tree variety (Lord Derby, Spartan, King of the Pippins, Bramley’s Seedling, D’Arcy Spice). The blocks were distributed across four tree rows, with each block occupying part of a single tree row (Fig. 5.1). Therefore, two blocks were located in the same tree row, however they were separated by 60 m. The location and lengths of experimental blocks were constrained by the locations and extent of each apple variety, hence it was necessary to include some blocks near the field edges. This potential bias was accounted for by alternating the arrangement of management treatments, and by testing distance from boundary as a fixed effect in the statistical models (described below).

Each block was between 42 and 60 m long by 3 m wide (the width of the tree row), the length of which was equally divided into two management treatments, comprising unmown vegetation to promote flowering ('flowering understoreys'), and a frequently mown treatment to suppress flowering ('mown understoreys') (Fig. 5.1, 5.2). The two treatments contained similar plant communities, having been sown with the same mix in 2014. In the mown understoreys, vegetation was cut as short as possible using a petrol strimmer initially in November 2019 and then approximately once per month over five occasions in spring/summer 2020, commencing on 24th April (Appendix 16). Cutting was undertaken immediately after sampling visits, to minimise any effects of disturbance on capture rates. The outer thirds of the flowering understoreys (and sections outside of the experimental areas) were cut once during the winter of 2019/2020 as part of standard farm operations, but were not cut during the 2020 growing season.

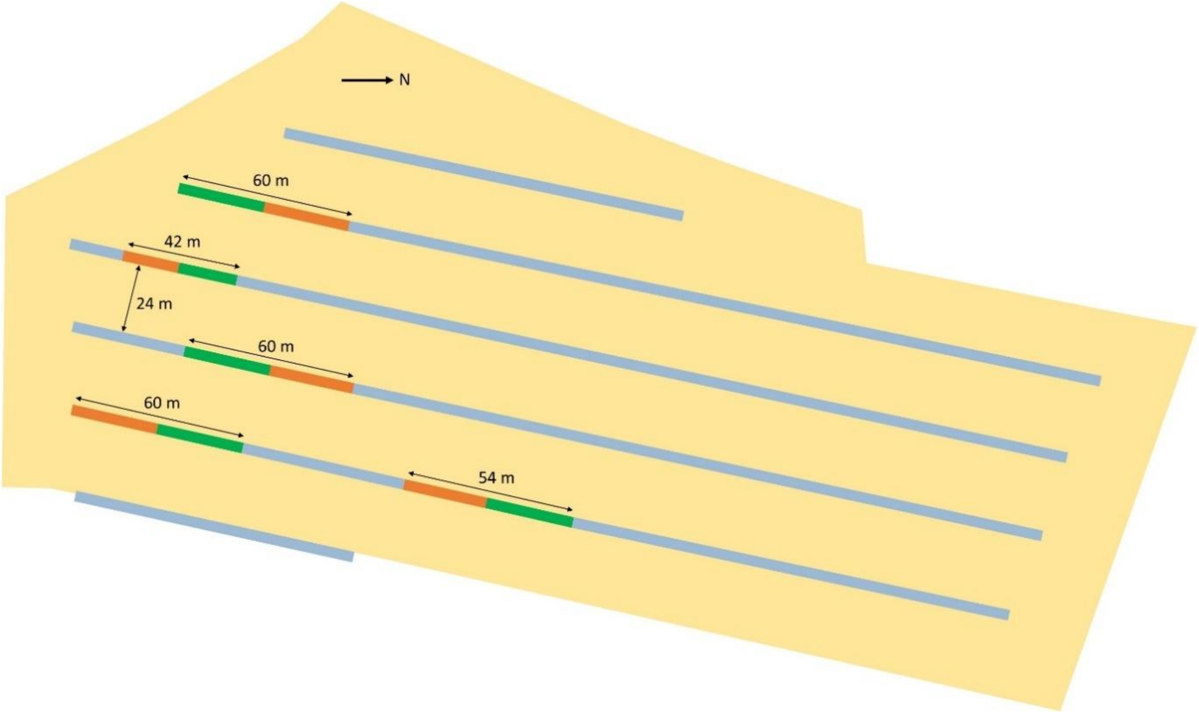

Figure 5.1. Schematic of the study field, where light orange = arable cropping, green = flowering understorey, orange = mown understorey, light blue = tree rows outside the experimental blocks, but subject to the same management as the flowering understoreys. All tree rows contained the same seed mix; treatments differed only in cutting frequency.

Figure 5.2. Photos of mown (left) and flowering (right) understoreys, taken in June 2020.

5.3.3 Sampling techniques

A variety of sampling techniques were used to address the objectives of the study (Table 5.1, Appendix 16). Each sampling technique was replicated four times within each treatment per block (Fig. 5.3), except arable yield samples which were replicated twice within each treatment block. This led to a total of 40 samples for each sampling technique (except arable yield), for each visit (4 sample locations x 2 treatments x 5 blocks). Pitfall traps, sticky traps, and grain samples were sited 0.5 m into the adjacent crop alley, to sample the effect of the understorey treatment on the adjacent crop and its invertebrate community. This distance was selected to minimise interference from other understorey treatments. Previous data from this site and two other sites showed limited spatial effects of diversity and richness metrics across alleys (Staton et al. 2021b), therefore samples at this distance can be expected to be broadly representative of the arable alley. No pitfall traps were installed within the tree rows because vegetation structure can bias capture rates (Thomas et al. 2006) and the ground-based invertebrate community is more relevant to the arable cropping area. Invertebrate specimens captured using pitfall traps and sticky traps were stored in a freezer and identified using an optical microscope. The taxonomic resolution selected for each taxon was that which was sufficient to establish functional group (see Appendix 5).

Table 5.1. Summary of sampling techniques used in the study. For further information on sampling methodology, see Appendix 16.

Purpose	Sampling technique	Temporal replication
Invertebrate natural enemies and pests in the tree component	Visual searches of trees	Eight visits between May and July
Apple pest and disease damage	Visual pest and disease assessment	One visit (July for diseases and pests except aphids, September for aphid damage)
Apple pollinators	Flower visitation counts	Two complete visits plus one partial visit to a block still in flower (late April and early May)
Apple pollination	Apple seed counts (Webber et al. 2020)	One visit in September
Apple yield	Fruit count and width	One visit in September
Invertebrate diversity, natural enemies, and pests^1 in the arable component	Pitfall traps (Lang 2000; Woodcock 2005)	Five visits (April, May, June, July, September)
	Sticky traps	Three visits (May, June, July)
Arable yield	Grain samples	One visit in August

[1] Arable pests were defined as those included in AHDB's field crop pest encyclopaedia (AHDB 2015).

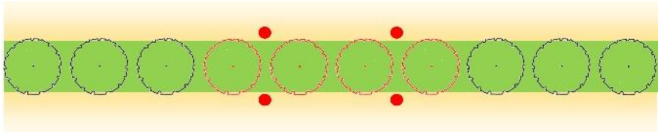

Figure 5.3. Arrangement of sampling locations within a representative treatment block. Trees outlined in red were sampled (visual searches for pests and natural enemies, pollinator visitation and seed counts), while the outer three trees (outlined in black) were unsampled buffer areas. The red dots represent sample locations within the adjacent arable alley (pitfall traps and sticky traps). The distance between each tree was 3 m.

5.3.4 Analysis

All analysis was undertaken using R version 3.5.2 (R Core Team 2018), with the packages lme4 (Bates et al. 2015) and MASS (Venables & Ripley 2002) used for model building. Prior to model building, the distribution of the response variable versus each fixed effect was visually inspected. Linear mixed models were used for data conforming to a normal distribution. Where the data was positively skewed, Poisson Generalized Linear Mixed Models (GLMMs) were initially applied. The residuals of the Poisson GLMMs were then inspected for heteroscedasticity, and negative binomial GLMMs fitted if necessary. Binomial GLMMs were used for proportion data, including apple pest damage and apple seed counts, fitted with an observation-level random effect to account for overdispersion. The significance of fixed effects was tested using the package 'lmerTest' (Kuznetsova et al. 2017).

Each response variable was visually explored for seasonal patterns in the data. Broadly, one of two types of model was then fitted (Table 5.2). The first model type was applied to response variables with possible seasonal effects, and aimed to assess understorey treatment effects over the season. The model therefore included a fixed interaction effect between understorey treatment and sampling visit, with the main effect for treatment removed. This approach allowed the effect of understorey treatment to be tested separately for each sampling visit. Sample block was included as a random effect. The second model type aimed to assess overall understorey treatment effects, where seasonal patterns were not apparent in the data. In this case understorey treatment was the single fixed effect, with two random effects comprising sample block and visit (where more than one visit was made). To account for potential effects arising from distance from field boundary, this was included as a fixed effect in GLMMs for invertebrate community or abundance response variables, where it was a statistically significant variable (p-value < 0.05), as shown in Table 5.2.

Taxonomic richness and Shannon diversity were calculated separately for pitfall traps and sticky traps using the most precise resolution in the dataset, including taxa at lower resolutions (e.g. family), in the R package 'vegan' (Oksanen et al. 2013). For the arable pest models, the data were subset to only include the sample method with the greatest capture rate for the response taxon, while sample visits with very low capture rates for the response taxon were excluded from the analysis if necessary to improve model fit.

Table 5.2. Model building specifications, showing which fixed and random effects were applied to each response variable. 'Treatment' fixed effect refers to understorey management (flowering or mown). The main effect of treatment was removed from the 'treatment vs visit interaction' model, to test treatment separately for each visit. Bracket symbols represent where the variable was applied to some models within that category.

		Fixed effects			Random effects	
Response	**Sample methods**	**Treatment**	**Treatment vs visit interaction**	**Distance from boundary**	**Block**	**Visit**
Pooled aphid colonies in apple trees – seasonal effects	Visual searches		•		•	
Pooled aphid colonies in apple trees – overall effects	Visual searches	•			•	•
Pooled natural enemies in apple trees	Visual searches		•		•	
Apple damage by aphids, other insects, and scab	Visual searches	•			•	
Pollinator visitation to apple flowers	Flower visitation counts	•			•	•
Apple seed count	Apple seed count	•			• (nested with sample tree)	
Apple yield	Apple yield	•			•	
Richness and Shannon diversity (separately for herbivores, natural enemies, pooled invertebrates)	Separately for pitfall and sticky traps		•	(•)	•	
Abundances of six arable pest taxa	See Appendix 17 (Table A17.6)	•			•	•
Pooled aerial insect captures	Sticky traps	•			•	•
Arable yield	Grain samples	•			•	

The effect of understorey treatment on the natural enemy community was investigated using partial redundancy analysis (pRDA) in the 'vegan' package (Oksanen et al. 2013). Natural enemy taxa were the response variables, understorey treatment and distance from field boundary were explanatory variables, and sampling block and visit were 'partialled out' covariables. Response variables were chord-transformed to account for the high proportion of zeros (Legendre & Gallagher 2001). Statistical significance was tested using the ‘anova.cca’ function in the ‘vegan’ package, using 9999 permutations. Effects on natural enemy traits were also investigated according to the same method, using an existing trait database (Staton et al. 2021b), but the results were not close to significance (p-value > 0.1) and are not presented. Similarly, the diversity of functional effect traits was investigated based on the approach in Greenop et al. (2018) and adapted in Staton et al. (2021b), but the results were not close to significance (p-value > 0.1) and are not presented.

Finally, we evaluated the financial implications of differing aphid damage to apple fruits (in the form of stunted fruit growth), mowing costs, and grant payments between understorey management treatments. Fruits were visually inspected for other damage including from other pests, moulds and diseases (see Appendix 16 for methodology), but the damage incurred did not significantly differ between management treatments (as set out in the Results) and they were therefore not included in the financial calculations, aside of omitting damaged apples from the alternative eating/cooking pricing scenario at Appendix 18. The income difference (ID, Equation 1) between flowering and mown understoreys was calculated as (i) the mean cost of aphid damage (CAD) to apples in mown understoreys minus the mean cost of aphid damage in flowering understoreys, plus (ii) the reduction in the cost of mowing (CM), assuming mown understoreys were cut five times per year and flowering understoreys once, with each cut costing £2.70 per ha of agroforestry (assuming tree rows occupy 10% of the field) (Lampkin et al. 2017), plus (iii) Countryside Stewardship AB8 grants (G) of £53.90 per ha of agroforestry for the flowering understorey treatment only, because this grant places restrictions on cutting frequency and timing.

$$(1)\ \mathrm{ID} = \mathrm{mean}(\mathrm{CAD})_{\mathrm{mown}} - \mathrm{mean}(\mathrm{CAD})_{\mathrm{unmown}} + \mathrm{CM} + \mathrm{G}$$

The cost of aphid damage (CAD, Equation 2) was calculated for each block by estimating potential yield (by assuming all aphid-damaged apples were fully developed and harvestable) minus actual yield, using predicted apple weights (W) (derived from measured apple widths, see Appendix 19 (Garratt et al. 2016b)), total apples per tree (TA), and aphid-damaged apples (AD) on each sample tree (T). These were measured according to the descriptions in Appendix 16. Yield loss to aphids per tree was then multiplied by trees per ha (TH), assumed to be 108, and apple price (AP), which comprised a heritage juice price of £1,600/t. This was based on the price that the study farm sold their juice to the public during 2020 (£4 per litre, assuming 2.5 kg of fruit produces 1 litre of juice). An alternative price scenario was also tested, comprising a conventional eating/cooking apple market using national average prices (Defra 2021) and excluding apples damaged by pests or disease (see Appendix 18). Variable costs of £376.80/t were subtracted from both price scenarios, to account for harvesting, packing, transport, and commission (Redman 2017). Separate calculations were performed for each sample block, followed by a mean across all varieties. All 'per hectare' values were based on a hectare of agroforestry, rather than a hectare of trees. Seed costs were not included in the calculations, because costs of flower mixes and standard permanent pasture mixes from major seed suppliers were comparable and therefore not expected to contribute to the income difference between understorey treatments.

$$(2)\ \mathrm{CAD} = ((\mathrm{W_T} * \mathrm{TA_T}) - (\mathrm{W_T} * (\mathrm{TA_T} - \mathrm{AD_T})) * \mathrm{TH} * \mathrm{AP}$$

5.4 Results

The understorey managements were successfully implemented, with the flowering and mown treatments becoming more visually different as the season progressed (Appendix 20). The flowering understoreys (and tree rows outside the experimental blocks) supported a diverse and abundant floral resource, particularly in late May and June. *Leucanthemum vulgare* flowers were particularly frequent, along with tall tussocky grasses such as *Dactylis glomerata* and *Deschampsia cespitosa*. The mown sections, although containing the same plant species, were characterised by a low grassy sward with sparse flowers throughout the study period. The barley in the crop alleys was sown in early April, which was later than intended due to wet weather, and although it did establish, its growth was hindered by a prolonged warm, dry period after sowing. The apple trees produced a successful harvest. The two trap-based sample methods (pitfall and sticky) captured more than 11000 specimens each, while the two in-field counting methods yielded 969 and 184 observations for apple pests / natural enemies and pollinators, respectively (Table 5.3).

Table 5.3. Total numbers of invertebrate specimens and taxonomic groups counted from each sampling method.

Sample method	Total count / number of specimens	Taxonomic groups
Apple pest and natural enemy visual counts	969 [1]	27
Pollinator counts	184	5
Pitfall traps	15318	121
Sticky traps	11899	74

[1] Aphids were counted by colony rather than per individual

5.4.1 Effects on functional groups, fruit damage and pollination in apple trees

Apple trees above flowering understoreys supported significantly fewer aphid colonies compared with mown understoreys, for pooled sample visits (Poisson GLMM, $z = -0.388$, p-value < 0.001). This effect was observed in all but one of the five sample blocks (Appendix 17 (Table A17.1)). Aphid colony numbers were significantly lower in trees above flowering than mown understoreys on three of eight sample visits, according to a separate model which used a sample visit interaction term (Fig. 5.4). *Dysaphis plantaginea* accounted for 82% of colonies, with other species comprising *Rhopalosiphum insertum*, *Dysaphis devecta* and *Aphis pomi.*

For the natural enemies in apple trees, we found a significant interaction between understorey management and visit number. Trees over flowering understoreys supported significantly more natural enemies in early May, but the pattern was reversed in late June (Fig. 5.4). Spiders (Araneae) were the most abundant group of natural enemies in apple trees, followed by earwigs (Dermaptera).

Apple fruit damage by aphids was significantly lower above flowering than mown understoreys (mean 13.0% damage above flowering versus 26.9% above mown understoreys, see Table 5.4 for model outputs). This effect was consistent for four sample blocks, while aphid damage was very low (<1% of fruits) in the remaining sample block. Apple damage from other insects or scab disease was not significantly affected by understorey management.

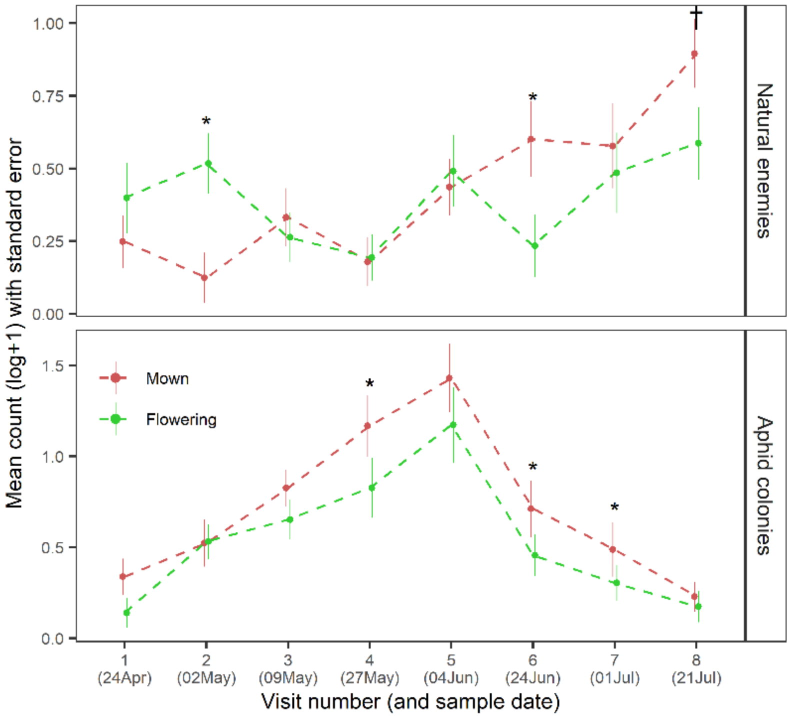

Figure 5.4. Number of aphid colonies and natural enemies on apple trees across the season, above mown and flowering understoreys. Bars represent standard errors. Symbols refer to p-values, where * < 0.05, † < 0.1. See Appendix 17 (Table A17.2) for model outputs.

Table 5.4. Effects of understorey management on apple damage, according to negative binomial GLMMs. Positive estimated regression parameters represent association with flowering understoreys. ‘Other insect damage’ includes *Cydia pomonella*, *Operophtera brumata*, and capsid damage, which were too infrequent to be analysed separately.

Apple damage	Estimate	Standard error	Z value	p-value	R^2 marginal	R^2 conditional
Aphids	-0.846	0.127	-6.678	<0.001	0.047	0.155
Other insect damage	0.093	0.237	0.392	0.695	<0.001	<0.001
Scab	0.002	0.163	0.009	0.993	<0.001	0.114

Pollinator visitation was significantly higher in apple trees above flowering understoreys than mown understoreys (Poisson GLMM, z = 2.220, p-value = 0.026). This effect was observed in four of the five sample blocks (Appendix 17 (Table A17.1)). *Apis mellifera* accounted for 86% of the pollinator visits, therefore a taxonomic analysis was not feasible. There was no significant effect of understorey management on the number of seeds per apple, which indicates pollination level (mean above flowering = 6.50, mown = 6.14, binomial GLMM, z = 1.560, p-value = 0.133), or on apple yield (mixed model, t = 0.982, p-value = 0.333).

5.4.2 Effects on the arable community and productivity

Shannon diversity and taxonomic richness of invertebrates captured in pitfall traps was significantly higher in crop alleys adjacent to flowering than mown understoreys in April and May, but over the following months this effect decreased and was not significant (Fig. 5.5, Appendix 17 (Table A17.3)). This early-season effect was more pronounced for natural enemies than herbivores, which showed no significant difference in any month (Fig. 5.5). The effect on natural enemies was consistent for all five sample blocks in May (Appendix 17 (Table A17.4)). There were no significant effects of understorey management on richness or diversity of sticky trap communities, in any month (Appendix 17 (Table A17.5)).

Thrips (Thyanoptera) were significantly less abundant in arable alleys adjacent to flowering than mown understoreys, and this effect was consistent for all sample blocks (Appendix 17 (Table A17.1)). None of the remaining five arable pest taxa showed a significant difference in abundance between understorey managements, although four of the taxa were less abundant in arable alleys adjacent to flowering than mown understoreys (Appendix 17 (Table A17.6)). However, overall insect captures on sticky traps were significantly lower adjacent to flowering understoreys (Poisson GLMM, estimate = -0.150, z-value = -8.180, p-value < 0.001), suggesting that insect movement rather than abundance may have been lower adjacent to the flowering understoreys.

Understorey management had no significant effect on natural enemy community composition in pitfall traps (F = 1.458, p-value = 0.089), although lycosid spiders had a relatively strong association with crop alleys adjacent to mown rather than flowering understoreys (Appendix 21). Barley yield sampled 0.5 m from the understoreys was not significantly affected by understorey management (mixed model, t-value = -0.197, p-value = 0.846).

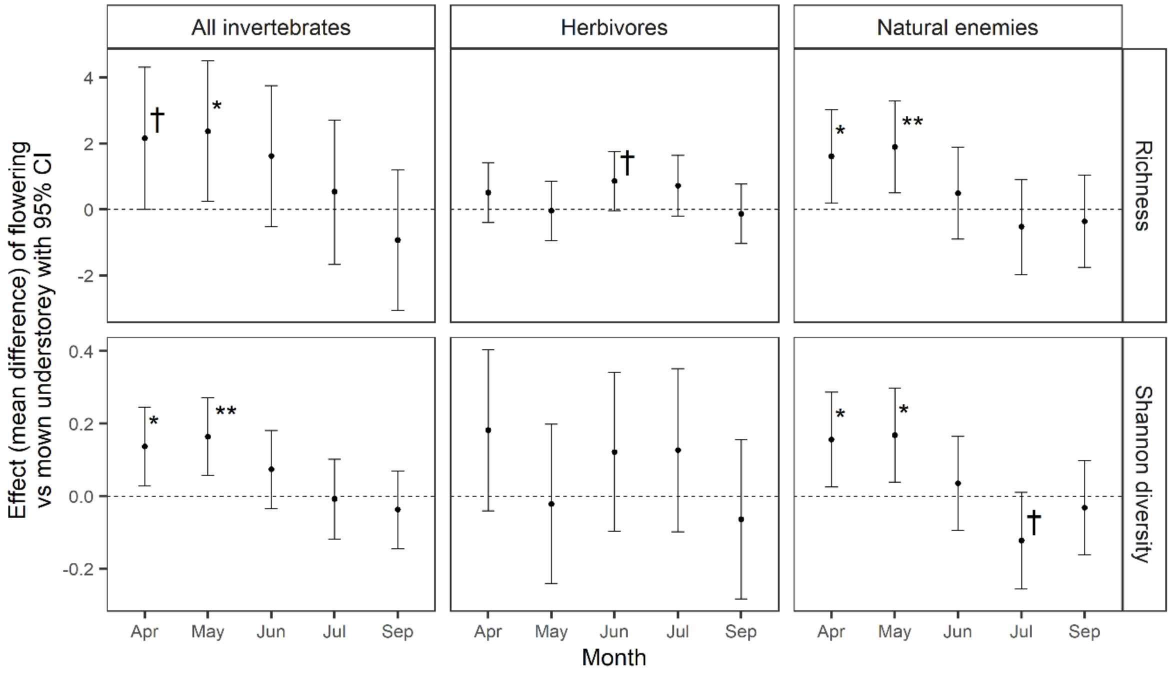

Figure 5.5. Effects of understorey management on invertebrate diversity and richness in pitfall traps. Effects are represented by mean difference between flowering and mown treatments, hence points above the dashed line (y=0) represent higher richness/diversity in arable alleys adjacent to flowering than mown understoreys. Effect sizes and confidence intervals are based on the outputs of mixed models where richness or diversity of each trophic level was the response variable, and the interaction between treatment and month was the fixed effect, with block as a random effect. Symbols refer to p-values, where ** < 0.01, * < 0.05, † < 0.1. See Appendix 17 (Table A17.3) for model outputs.

5.4.3 Financial modelling

According to our financial model of apple damage by aphids, mowing costs, and Countryside Stewardship grants, flowering understoreys increased farm income by a mean of £231.02 per ha of agroforestry, when basing income on heritage juice prices that were equivalent to those currently achieved at the study site. This compares to a mean increased income of £167.99 per ha under a hypothetical eating / cooking market (Appendix 18). There was large variation among sample blocks, because aphid damage between management treatments differed for each block, with the largest effect observed for the Lord Derby variety. Aphid damage to apples was the major contributor to income differences, followed by grants from Countryside Stewardship, while mowing costs had a minor contribution (Table 5.5).

Table 5.5. Predicted changes in income (£/ha of agroforestry) arising from using a flowering understorey relative to a mown understorey. Positive values represent higher income (or less cost) from using the flowering understorey. Flower mix grants are for Countryside Stewardship AB8. The 'Spartan' block results should be interpreted with caution, because aphid damage was very low (< 1%). u/s = understorey.

Apple variety	**Predicted increase in income from reduced apple yield loss to aphids**	**Income from flower mix grant**	**Reduction in mowing costs**	**Total predicted increase in income from flowering u/s relative to mown u/s**
Lord Derby	580.22	53.90	13.50	647.62
Spartan	-11.69			55.71
King of the Pippins	-32.23			35.17
Bramley's Seedling	173.72			241.12
D'Arcy Spice	108.07			175.47
Mean	163.62	53.90	13.50	231.02

5.5 Discussion

Our results showed that the flowering understoreys delivered multiple benefits for invertebrate diversity and associated ecosystem services, compared with mown understoreys which comprised the same plant community but were subject to frequent cutting. In trees above flowering understoreys, natural enemy abundance was significantly higher in early May, while aphid colonies and aphid-damaged fruits were significantly less numerous overall. In addition, pollinator visitation to apple flowers was significantly higher in the trees above flowering understoreys. Arable alleys adjacent to flowering understoreys supported significantly higher Shannon diversity and taxonomic richness of ground-based invertebrate natural enemies early in the season. There were also some indications of pest suppression in alleys adjacent to flowering understoreys, however this result should be interpreted with caution because it could be affected by sampling method biases. Flowering understoreys were predicted to improve farm income compared with mown understoreys, according to our case study financial model of aphid damage, mowing costs and grant payments.

5.5.1 Effects in the apple trees: natural pest control and pollination

We found that flowering understoreys increased natural enemy abundance in apple trees early in the season, reduced aphid colony density, and reduced the number of apples lost to aphid damage, which is supported by previous research of flower strips in insecticide-free apple orchards (Cahenzli et al. 2019; Herz et al. 2019). However, to our knowledge, this study is the first to report lower apple damage at harvest and, as a consequence, financial benefits of flowering strips for apple production. This could be because damaged fruits were not removed as part of farm management in this study, whereas fruit thinning in previous studies could have masked any effect on fruit damage (Cahenzli et al. 2019). Bottom-up mechanisms could play a role in aphid suppression, for example flowering understoreys could intercept more water, reducing uptake by trees, which reduces aphid attraction (Rousselin et al. 2017). A more plausible mechanism for aphid suppression above the flowering understoreys could be the higher natural enemy abundance early in the season, given the importance of early-season control for aphid growth (Rousselin et al. 2017), while spider abundance the previous autumn has been linked to rosy apple aphid control (Cahenzli et al. 2017).

The early season benefit of flowering understoreys to arboreal natural enemies could be attributable to favourable shelter conditions during winter, and/or the availability of alternative prey sources in the understorey early in the season and at the end of the previous year (reviewed in Pfiffner & Wyss 2004). We found higher natural enemy abundance above mown than above flowering understoreys later in the season, possibly because higher aphid colony density attracts aphidophagous predators (Cahenzli et al. 2019). However, these aphid colonies quickly die off before autumn, and the flowering understoreys are likely to support higher availability of alternative non-pest prey (Pfiffner & Wyss 2004; Wyss 1996). Although we could not disentangle the relative contributions of different natural enemy taxa, previous studies of flower strips in orchards have found contrasting roles of different natural enemy guilds in suppressing aphids (Cahenzli et al. 2017, 2019), suggesting that the promotion of the whole natural enemy community is the most promising solution (Rousselin et al. 2017).

The lack of significant effects of understorey management on apple damage from other pests such as *Cydia pomonella* is consistent with the current literature of flower strips in orchards, where effects on *C. pomonella* damage are weak and inconsistent, and vary among studies and study years (Cahenzli et al. 2019; Markó et al. 2012; Sigsgaard 2014). We also found no significant effects of understorey management on apple scab, although there appears to be a lack of evidence as to the effects of flower strips in orchards on this disease.

Agroforestry systems have been shown to increase the abundance and species richness of pollinators and pollination of phytometers relative to monoculture controls (Staton et al. 2019; Varah et al. 2020). Our findings suggest that understorey management is an important factor driving this effect. We found higher pollinator visitation to apple flowers above flowering than mown understoreys, despite a sparse flower resource in the understorey at the time of apple flowering and the small scale of the plots compared with the foraging distances of pollinators (Gardner et al. 2020). Nevertheless, this result is supported by studies of apple orchards where flower cover increased pollinator visitation (Campbell et al. 2017; Samnegård et al. 2019). The lack of corresponding effect on apple pollination is also supported by a previous study of apple orchards, which found that although flower strips increased pollination visitation, apple fruit set was more strongly related to wild insect richness and andrenid bee visitation, neither of which responded to the presence of flower strips (Campbell et al. 2017). Understorey management could influence the availability of bee nesting resources such as bare ground and tussocks at larger spatial scales, given that the dominant pollinators in UK apple orchards tend to be ground-nesting bees (Garratt et al. 2016a), although this was unlikely to affect our results at the temporal and spatial scales of this study. Furthermore, the high proportion of *Apis mellifera* in our data suggests that the effect was driven by attraction to the foraging rather than nesting resource. The inclusion of flowering understoreys into agroforestry systems could improve yield and/or quality of pollination-dependent arable crops such as oilseed rape, which receives higher pollination service adjacent to flower strips (Sutter et al. 2018). In addition, flowering understoreys could improve the long-term stability of pollinator populations and pollination service by providing seasonal continuity of floral resources (Timberlake et al. 2019).

5.5.2 Effects in the arable crop: invertebrate diversity and natural pest control

Our finding of significantly higher richness and Shannon diversity of natural enemies in flowering versus mown understoreys early in the season is consistent with findings from flower strips in arable fields (Ditner et al. 2013; Tschumi et al. 2016). Various mechanisms have been proposed to explain how flower strips can benefit natural enemies, including provision of shelter during winter, nectar and pollen, and alternative prey or hosts (Gurr et al. 2017). The stronger effect early in the season, prior to any substantial flowering, suggests that the vegetation structure during winter was a more important driver than flowering resources such as nectar and pollen, albeit this was only over one season. This is consistent with a study which found that overwintering natural enemies were more associated with understorey vegetation strips than crop alleys in an agroforestry system (Boinot et al. 2019b). In addition, flower strips with high vegetation cover and plant diversity have been shown to be important for overwintering ground-based natural enemies and pollinating flies (Ganser et al. 2019), while tussocky grass cover is important for the functional diversity of overwintering carabid beetles (Woodcock et al. 2010).

We also found significantly fewer thrips in arable alleys adjacent to flowering compared with mown understoreys. However, pooled sticky trap captures were significantly lower adjacent to flowering than mown understoreys, which could be explained by flowers ‘competing’ with sticky traps for insect visitation. Similar biases have been reported in pollinator sampling using pan traps (O’Connor et al. 2019). Therefore, we would recommend additional sampling methods such as visual counts or damage assessments in future studies to confirm this finding. Nevertheless, the findings potentially indicate an improved level of natural pest control adjacent to the flowering understoreys. Arable crop yields did not significantly differ between understorey treatments, providing no evidence for any short-term reduction of crop pest damage adjacent to flowering understoreys. This is consistent with a meta-analysis of flower strips in agriculture, which found that although flower strips significantly increased pest control services, there was no significant effect on crop yield (Albrecht et al. 2020). In the longer-term, the higher richness and diversity of natural enemies adjacent to flowering understoreys could improve the stability and resilience of this ecosystem service to environmental change (Dainese et al. 2019; Jonsson et al. 2017).

5.5.3 Financial implications

Our financial model found that flowering understoreys improved farm income compared with mown understoreys, because of the lower apple damage by aphids (mean income increase of £163.62), grant payments (mean income increase of £53.90) and lower mowing costs (mean income increase of £13.50, all per ha of agroforestry). The overall mean income increase of £231.02 compares to a forecasted gross margin of £1,962 per ha for a wheat-apple agroforestry system at peak production, adapting the gross margin by Briggs and Knight (2019) according to the mean apple yields and price applied in our study. An alternative pricing scenario based on a conventional eating/cooking apple market also predicted higher income arising from flowering than mown understoreys, although the increase was slightly reduced (£167.99 per ha of agroforestry, see Appendix 18), because of the lower apple prices.

Therefore, lower aphid damage provides a financial incentive for the adoption of understorey management to promote flowering, although the potential for ecological disservices such as rodent damage and weed competition requires further assessment. The minor contribution of mowing costs to the financial output suggests that flowering understoreys would have similar financial benefits over an intermediate management regime, for example with two or three cuts per year, assuming similar levels of aphid damage to the mown management in this study. Our results suggest that specialised heritage juicing is a favourable option for these agroforestry systems, because of the potential to attract premium prices and the inconsequence of fruit appearance.

5.5.4 Constraints

It is important that the dispersal ability and movement patterns of species are taken into account in the interpretation of results from plot-scale studies (Merckx et al. 2009; Prasifka et al. 2005). The effects we find in this study could be less than those achievable under field-scale conditions because of insect movement between treatments and into and out of experimental blocks (Bennett & Gratton 2012; Prasifka et al. 2005). Furthermore, the scale of the study is considerably less than typical pollinator dispersal distances (Gardner et al. 2020), which would mask any effects of nesting resource availability. This was a one-year study, therefore stronger contrasts between the two management regimes might be expected over a longer time period. Nevertheless, the understorey vegetation was established six years prior to the study and subsequently managed to promote flowering, giving time for species to colonise and populations to establish, for example six years is beyond the time at which pollination services are maximised with flower strip age (Albrecht et al. 2020). Our financial model is based on a case study over a single year and does not take into account other factors such as long-term tree growth and productivity, and should therefore be interpreted with caution.

5.5.5 Potential disadvantages of flowering understoreys

Although we found multiple benefits of flowering understoreys for invertebrate diversity and associated ecosystem services, from a wider perspective there are a number of potential disadvantages. For example, flowering understoreys could increase rodent pest densities, competition with the trees for resources such as water and nutrients, spread of weeds, frost damage to apple trees, and labour to collect windfall apples (Pfiffner et al. 2018; Reubens 2018). To some extent, appropriate management such as timing of the annual cut could help to mitigate these disadvantages (Pfiffner et al. 2018). These factors require further economic assessment and should be considered when developing management options.

5.5.6 Recommendations for future research

Given these findings, we recommend that future studies which aim to evaluate the effects of alley-cropping agroforestry systems on biodiversity take into account understorey management and its interaction with season, which could be key factors influencing the previously observed heterogeneity in effects (Pumariño et al. 2015; Staton et al. 2019). In addition, the scale of plot manipulation should be considered, given species movement patterns, as discussed above. Finally, studies should aim to quantify the results in ways which are meaningful to practitioners, such as yield and profit (Kleijn et al. 2019).

5.5.7 Conclusions

This study is the first to demonstrate the value of flowering understoreys in a silvoarable system for invertebrate richness and diversity, associated ecosystem services, and farm income. Flowering understoreys increased predator densities in apple trees, decreased aphid colony growth, decreased aphid damage to apples, and increased pollinator visitation to apple flowers, while increasing ground-based natural enemy diversity in the adjacent arable crop. Therefore, flowering understoreys appear to be a win-win management option in terms of biodiversity, associated ecosystem services, and farm income, although wider issues such as resource competition between understorey vegetation and trees should also be considered. We recommend that understorey management is taken into account in studies of biodiversity in alley-cropping systems, and recommend further confirmation of these results at other sites and at larger spatial scales.

5.6 Data availability

The data presented in this chapter are openly available in NERC’s Environmental Information Data Centre at https://doi.org/10.5285/83a10b11-23ef-4378-a56d-c63cce365275.

6. Productivity, biodiversity trade-offs, and farm income in an agroforestry versus an arable system

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This final data chapter draws together findings from previous chapters, including data on weed and pest abundance in Chapter 3, to evaluate the productivity and farm income of the studied agroforestry system relative to monocultures. The costs and benefits of biodiversity are evaluated in terms of weed and pest associations with yield, and apple pollination metrics.

6.1 Abstract

The uptake of diversified farming systems is constrained by a scarcity of evidence regarding financial costs, benefits, and risks. Here, we evaluate the productivity and projected farm income of an agroforestry system, where apples are integrated with arable crops, by combining primary data with ecosystem service and cost-benefit models. Our ecosystem service assessments included: 1) weed and pest associations with arable yields; 2) apple seed set as a proxy for pollination, and; 3) carbon sequestration. Arable yields were up to 11% lower in agroforestry than arable systems, and were significantly negatively associated with weed cover in both systems. Apple yields in agroforestry were similar to typical yields from comparable orchards. Apple seed set was significantly higher in agroforestry than conventional orchards for one of two varieties. Predicted gross mixed income was higher in agroforestry than arable systems in 15 of 18 productivity scenarios over 20 years, which was supported by a case-study. Apple yield and price were the major determinants of gross mixed income. Payments for carbon sequestration were predicted to contribute 47% to 88% of agroforestry establishment costs. This study demonstrates how a diversified farming system can improve farm income, but grant support would reduce the initial negative cash-flow.

6.2 Introduction

Diversified farming systems have been proposed as a potential means of reducing the environmental harm of agriculture without compromising productivity, through sustainable, or ecological, intensification (Kremen & Miles 2012; Rosa-Schleich et al. 2019). Despite this, the promotion and adoption of diversified farming systems have seen limited uptake in temperate regions, which is thought to be in part due to a scarcity of evidence regarding the financial costs, benefits and risks relative to conventional non-diversified farming (Kleijn et al. 2019; Rosa-Schleich et al. 2019). Therefore, comparative cost-benefit analyses of these systems at relevant spatial and temporal scales are needed to inform policy and stimulate uptake.

Agroforestry is a diversified farming system which involves the intentional integration of productive trees or shrubs into agricultural land. Relative to monocultures, agroforestry systems can enhance biodiversity and multiple ecosystem functions and services (e.g. Smith et al. 2013a; Torralba et al. 2016; Tsonkova et al. 2012; Udawatta et al. 2019). These include marketable services such as natural pest control, pollination, and carbon sequestration (Pumariño et al. 2015; Staton et al. 2019; De Stefano & Jacobson 2018), but also disservices such as higher abundances of some pest taxa (Staton et al. 2019, 2021b). The relative benefits and costs of these services and disservices to productivity and farm income are not clear.

Farmers, landowners and other stakeholders perceive environmental factors such as biodiversity and soil conservation as positive aspects of agroforestry systems in temperate regions, while cashflow and management costs are seen as negative factors (García de Jalón et al. 2018; Valdivia et al. 2012). A lower proportion of farmers in northern Europe compared with the south have a positive perception of the profitability of silvoarable systems (agroforestry in arable settings) (Graves et al. 2008). A survey of farmer perceptions in the UK towards a poplar silvoarable system reported that although most had negative perceptions of its profitability, and there was concern that tree rows could become sources of pests and weeds, 20% would adopt this system if convinced of its higher profitability compared with conventional arable production (Graves et al. 2017). Furthermore, a recent survey of readers of the UK's Agroforestry Handbook identified a need for financial modelling of agroforestry systems (Raskin 2020).

Economic modelling of silvoarable systems has a long history (reviewed in Graves et al. 2005). More recently, the Farm-SAFE economic model, primarily intended for timber silvoarable systems, was developed under the Silvoarable Agroforestry for Europe (SAFE) project (Graves et al. 2007, 2011). This model facilitated a series of studies which aimed to evaluate the economic performance of silvoarable relative to arable systems in Europe and Canada. These studies consistently concluded that the farm business profitability of timber silvoarable relative to arable systems was dependent on high value timber trees such as walnut, high timber prices, grant support, or low discount rates (Graves et al. 2007; Palma et al. 2007b; Sereke et al. 2015; Toor et al. 2012; Van Vooren et al. 2016).

Ecosystem service valuations are widely used to demonstrate the added value of environmental benefits of diversified farming systems such as agroforestry. According to recent modelling studies, agroforestry systems can theoretically be more profitable than conventional alternatives after accounting for payments for ecosystem services (or reductions in disservices), including carbon sequestration, reduced greenhouse gas emissions, reduced loss of nutrients and soils, higher groundwater recharge, and reduced pollination deficit (García de Jalón et al. 2017; Giannitsopoulos et al. 2020; Kay et al. 2019a).

Nevertheless, cashflow remains a major constraint associated with timber silvoarable systems, because of the time taken for trees to reach harvest, which even for the fastest growing trees is expected to be 20 years (Graves et al. 2007). Furthermore, timber trees might not be eligible for agricultural subsidies and could be subject to legislative requirements for replanting after harvest. These constraints are particularly pertinent to farmers on short-term tenancies, which are especially prevalent in Europe. For example, between 32% and 74% of agricultural land is tenanted in the UK, Germany, and France, with an average tenancy of between 5 and 11.5 years (Ciaian et al. 2012), which is not feasible for timber production.

An alternative form of silvoarable agroforestry is orchard intercropping, where fruit trees such as apple are integrated into arable or pasture (Bhardwaj et al. 2017). Although these systems have historic origins, they have been gaining renewed attention recently as an alternative to timber silvoarable systems, because of their potential to deliver a more rapid return on investment (Gao et al. 2013; Newman et al. 2018; Smith et al. 2016). One innovative example of this system comprises intercropping arable crops with apple trees on appropriate rootstocks (e.g. MM106) to limit their height and subsequent shading impacts on the arable crop, while being reasonably competitive with surrounding ground vegetation. Late-fruiting varieties are selected so that the apple and arable harvests are temporally separated. Typically, single rows of apple trees are intercropped with arable alleys, which are in most cases 24 m wide to facilitate access by modern farm machinery. There has been increasing uptake of this agroforestry system in recent years, particularly in the UK (Newman et al. 2018), despite any studies of its financial performance.

In this study, we aimed to evaluate the productivity, gross mixed income, and contribution of marketable ecosystem services and disservices in this apple-arable agroforestry system, relative to conventional arable systems that consist of a yearly rotation of crops in monoculture. We selected three ecosystem services / disservices based on the availability of empirical data and/or existing models, comprising (i) arable pest and weed pressure, which has been identified as a potential cost of agroforestry by UK arable farmers (Graves et al. 2017); (ii) pollination, which is important for the quality and quantity of apples produced, for example in the absence of pollination, apple yield is reduced by around 55 to 60 % (Garratt et al. 2014;

Webber et al. 2020); (iii) carbon sequestration and reduced emissions. We combined primary data collection with a series of ecosystem service and cost-benefit analysis models to explore the following research questions:

1. Does arable crop yield differ between the agroforestry system and arable controls, and is this associated with invertebrate pest abundance and weed cover?
2. How does apple yield in the agroforestry system compare with typical orchard yields, and does apple pollination differ between agroforestry and orchard systems?
3. What is the value of carbon sequestration and reduced emissions in the agroforestry system compared with the arable controls?
4. Theoretically, how does gross mixed income of the agroforestry system compare with arable controls, how does empirical case-study data compare to these theoretical expectations (cost-effectiveness analyses), and which factors most strongly influence gross mixed income (sensitivity analysis)?

6.3 Methods

6.3.1 Arable yields and associations with pests and weeds (Question 1)

To compare crop yields between the agroforestry and arable systems, we sampled cereal yield (scaled up to tonnes per hectare) from three UK sites (see Appendix 3). Each site was a working farm containing (i) an agroforestry field, configured in an alley-cropping arrangement where single tree rows were intercropped with 24 m wide arable crop alleys, and (ii) an arable field under the same management. Two years (i.e. two harvests) of data were collected for each site, between 2018 and 2020. The sampled cereal crops comprised winter oats (2 sites), winter wheat (2 sites) and spring barley (1 site). At each site, samples were collected from 12 points in the agroforestry field, located 0.5, 5 and 9.5 m from the tree row, and from 16 points within the arable field following the same pattern around ‘virtual’ tree rows with additional samples at 0 m. Each grain sample was taken from a 50 x 50 cm quadrat, within one week of the field harvest commencing. Samples were threshed using a Wintersteiger Hege 16 and then weighed. Models were built to test the effect of farming system (agroforestry versus arable), crop type and distance from tree row on yield (Table 6.1).

Table 6.1. Variables and data subsets used to build linear models, mixed models, and generalised linear mixed models. 'Farming system' refers to agroforestry versus arable/orchard. Analysis was undertaken in R version 3.5.2 (R Core Team 2018) using the 'lme4' package (Bates et al. 2015). OLRE = observation-level random effect, to account for overdispersion.

Response	**Fixed effects**	**Random effects**	**Subset**	**Family**
Grain weight	Interaction between farming system, and crop type (barley/wheat or oats), with main effect for farming system removed	Site, year	-	Gaussian
Grain weight	Distance from tree row	Site, year	Agroforestry	Gaussian
Grain weight	Farming system, weed cover, slug abundance. Separate models to test interaction between farming system and weed cover or slug abundance.	Site, year	Slug data filtered to only include pre-harvest records.	Gaussian
Apple seed counts	Year (as factor)	Site, OLRE	Orchards, separate model for each variety	Binomial
Apple seed counts	Farming system	Site, OLRE	Separate model for each variety	Binomial
Apple seed counts	Farming system, pesticide use (binary)	Site, OLRE	Separate model for each variety	Binomial
Equivalent annual value (EAV)	Farming system	-	-	Gaussian

A previous study found higher slug abundance and non-crop plant cover in agroforestry crop alleys compared with arable fields (Staton et al. 2021b), using data collected from the same sample locations as the yield data in this study. Therefore, to investigate possible effects on yield, we tested associations between these two taxa with arable yield using mixed models (Table 6.1).

6.3.2 Apple pollination and yield (Question 2)

We sampled apple fruits from four UK agroforestry sites in August and September 2020 (Appendix 3). At each site, between 40 and 100 apples were sampled to record maximum width and number of seeds. The number of fruits on each sampled tree was also recorded, except at the Norfolk site where the apples had already been harvested. We sampled two varieties: Bramley (a large culinary apple) from all four sites, and Braeburn (desert apples) from two sites (Appendix 3). An equal number of Bramley and Braeburn were sampled at the latter two sites.

We estimated apple yield at each site based on the number of apples per tree and predicted apple weight, derived from the relationship between width and weight for both varieties in Garratt et al. (2016b) (Appendix 22). Predicted yields were compared with expected yields in the Organic Farm Management Handbook (Lampkin et al. 2017), because none of the apples in the agroforestry sites were treated with pesticides.

Seed counts per apple are a proxy for pollination service (Garratt et al. 2016a; Webber et al. 2020). Therefore, to compare pollination service, the seed set per apple from the agroforestry sites was compared with previously published orchard data in Garratt et al. (2016b). To compare this orchard dataset to 2020 conditions, we sourced 30 each of non-organic and organic Bramley, 40 non-organic Braeburn and 40 organic Braeburn apples from a wholesaler. These originated from orchards in Kent, UK, however no UK source was available for organic Braeburn, so this was sourced from Lower Saxony, Germany, which is climatically very similar to Kent. Maximum width and number of seeds were measured in these fruits.

The effect of year on seed count in orchard apples was tested using binomial GLMMs for each variety (Table 6.1). Year had no significant effect (Appendix 23); therefore, 2016 and 2020 data were combined to test the effect of farming system (agroforestry versus orchard systems) on seed counts for each variety (Table 6.1). We also ran a separate model with pesticide use (organic/no-spray or conventional) as an additional fixed effect, although only one organic orchard site was available for each variety.

The value of pollination was estimated using formulae adapted from Garratt et al. (2014) (Appendix 22), which compares pollination value between two treatments (in this case agroforestry versus orchard systems) based on differences in fruit set and weight. To control for confounding factors which could affect apple fruit set, weight and width, such as soil type, climate and management, only seed count data was used as empirical data input. Apple width, weight and fruit set were estimated using their relationships with seed count, based on the data in Garratt et al. (2016b) for each variety.

6.3.3 Carbon emissions and sequestration (Question 3)

To predict carbon dioxide emissions and sequestration, we primarily used the Farm Carbon Calculator (Farm Carbon Toolkit 2020), which is a web-based carbon calculator, underpinned by peer-reviewed evidence, designed to assess emissions and sequestration on UK farms. We focussed on two factors: emissions from crop residues and sequestration from fruit trees. We took a conservative approach by not incorporating other factors such as machinery movements and inputs, because although these are likely to be reduced in the agroforestry system, there is uncertainty depending on management of the tree rows. Soil carbon stocks vary little between agroforestry and arable systems, according to recent modelling, so were not included here (Giannitsopoulos et al. 2020).

Reduction in emissions from crop residues depends on crop type and yield, so was modelled separately for each of three productivity levels (low, average and high, described further in Section 6.3.4), management system (conventional or organic) and crop type. Sequestration from fruit trees was based on the area they occupy (9.2%) in the modelled agroforestry system described at Section 6.3.4. The amount of carbon dioxide sequestered by apple trees, including below-ground sequestration, was assumed to be 3.3 or 5.0 t CO_2e/ha/year (Farm Carbon Toolkit 2020; Page 2011).

For each productivity scenario, we calculated the net difference in greenhouse gas emissions/sequestration, i.e. emissions in arable minus agroforestry systems, plus sequestration in the agroforestry system. Two scenarios for greenhouse gas (CO_2e) values were evaluated: (i) traded EU allowances, which reflect current and projected trading prices, and (ii) non-traded shadow price of carbon. The latter incorporates discounted future social costs of greenhouse gas emissions and can be interpreted as the government's willingness to pay for reductions in carbon emissions. Carbon prices were sourced from the UK's Green Book Supplementary Guidance (Department for Business, Energy & Industrial Strategy, 2019) and covered the period 2020 to 2039 to reflect predicted increases in carbon value over the next 20 years.

6.3.4 Gross mixed income (Question 4)

Financial cash-flow was quantified as gross mixed income (GMI), because this represents the most relevant outcome for small family businesses by representing joint income from their unpaid labour and capital investments, unlike profit which deducts all labour costs and is more relevant to corporations. The most established field site from which we collected empirical arable and apple data was used as a model system to investigate farm income (i.e. GMI) and the contribution of marketable ecosystem services, relative to an equivalent arable system. This site was Whitehall Farm, Cambridgeshire, UK (described in Newman et al. (2018)), where an agroforestry system was planted across approximately half of the farm (52 ha) in 2009, with the remainder retained as monoculture arable land. The modelled agroforestry system and arable controls were based on a theoretical 16 ha field (Appendix 24), which is the average field size in Cambridgeshire, where over 80% of farmed land is arable (Robinson & Sutherland 2002). We analysed economic performance over a 20 year period, because this is the typical duration of dessert apple trees (Redman 2017).

To compare the financial performance of the agroforestry system compared with arable controls, we used the xlwings library in Python version 3.7.4 (Python Software Foundation 2019) to manipulate inputs into the Excel-based Farm-SAFE economic model (Graves et al. 2007, 2011). Model outputs were similarly extracted with Python and plotted using the 'ggplot2' package in R version 3.5.2 (R Core Team 2018; Wickham 2016). The current value of future GMI was calculated as net present value (NPV, Equation 1), by reducing costs and benefits that occur in future years (Equation 2) by an annual discount rate, which was set at 3.5% (HM Treasury 2018).

$$(1)\ NPV = \sum_{y=1}^{n} \left(\frac{GMI_y}{(1+r)^y} \right) - i$$

Where GMI = annual gross mixed income (Equation 2), i = capital investment costs based on scaled costs of orchard establishment (see Appendix 26), n = total number of years (20, which is the typical duration of dessert apples (Redman 2017)), r = discount rate (3.5%), and y = year after present (year 0).

$$(2)\ GMI = (yield \times price) + subsidies - variable\ costs - fixed\ costs$$

In Equation 2, yield and price represent both the apple and arable components of the system (explained below). Apple yields were reduced in the first five years to account for establishment. Subsidies comprised Basic Payment Scheme (in England) plus greening, plus Countryside Stewardship organic payments for organic systems, and were equivalent for the agroforestry and arable systems (except for the case study, explained in the corresponding section below). Variable costs included seed, fertiliser, sprays, and casual labour, plus annual pruning and harvesting of apple trees and removal of apple trees in year 20. Fixed costs included paid and casual labour, machinery, overheads, and rent. Further information on these parameters is provided in Appendix 26.

We also calculated equivalent annual value (EAV, Equation 3), which represents NPV in annual terms (parameters are defined in Equation 1):

$$(3)\ EAV = \frac{NPV \times r}{1 - (1+r)^{-n}}$$

All analyses used Euro currency for consistency with the Farm-SAFE model and previous associated publications, using an exchange rate of £1 = €1.18 based on the Bank of England's spot exchange rate for the end of 2019 (Bank of England 2020). Outputs are converted to pound sterling in Appendix 25.

Theoretical GMI

We tested the theoretical GMI of the agroforestry versus arable systems using farm management handbooks, which provide cost, yield and price figures for low, average and high levels of production, reflecting farm-dependent factors such as soils, climate and farmer expertise (Lampkin et al. 2017; Redman 2017). As the productivity level of combinable crops is not necessarily related to the apple crop, we modelled each combination of productivity level, for each management system (conventional versus organic). Therefore, 18 productivity scenarios were modelled (3 combinable crop yield levels x 3 apple yield levels x 2 management systems). In each scenario, the financial performance (NPV and EAV) of the agroforestry system was compared with the equivalent arable system.

Apple harvest costs (e.g. harvesting and packing, see Appendix 26) were calculated per tonne of harvested apples. Otherwise, all parameters other than yield remained constant among productivity levels (Appendix 26). The modelled conventional system was based on rotation of two years of winter wheat followed by a third year of oilseed rape (OSR). This is a widely used crop rotation in Europe, for example, OSR covered 380000 ha in the UK in 2020 (Defra 2020), suggesting that this rotation occupies approximately 1 million ha in the UK (assuming OSR recurs every three years). The modelled organic system comprised a six-year rotation of red clover, winter wheat, winter oats, spring beans, winter triticale, and spring barley, which has been recommended as a balanced rotation in the UK (HGCA 2008). In all cases, the crops grown in comparable agroforestry and arable systems were the same, so that only the presence of agroforestry tree rows and the area occupied by combinable crops differed between the two systems.

Case study

Annual records of apple and combinable crop yields in the agroforestry and arable fields, collected by the farm manager at the Whitehall Farm site, were used to empirically test the GMI of the agroforestry versus arable systems. Because different fields within the farm are at different stages of rotation, we ran 1000 Monte Carlo simulations, with the crop rotation in each simulation randomised based on the proportion of crops in the actual rotation (Appendix 27). The same crop type was applied to agroforestry and arable fields in each year. For each year, in each simulation, apple and combinable crop yields were randomly sampled from a normal distribution based on the mean and standard deviation of the empirical yield data. Equal arable yields were applied to each farming system, to reflect the comparable yields between farming systems at this site. Initial establishment costs were 1357 €/ha, based on actual data from Whitehall Farm. Fertiliser and apple protection (pesticide) costs were not included to reflect farm practices. A Countryside Stewardship AB8 grant (€636.02 per ha of trees) was included for the tree row flowering understorey, and establishment costs included. Otherwise, model parameters were applied according to the organic system at Appendix 26. The effect of farming system on GMI (represented by EAV) was tested using a linear model (Table 6.1).

Sensitivity analysis

To investigate the sensitivity of GMI in the agroforestry system, the above case study analysis was run under the following scenarios (1000 simulations for each scenario): (i) low arable yields, reduced by 11.4% in the agroforestry system (based on barley/wheat yields in Section 6.4.1); (ii) low apple yields, comprising the lower estimate of observed agroforestry yields (4 t/ha, from the Whitehall Farm case study); (iii) high apple yields, comprising the upper estimate of observed agroforestry yields (14.84 t/ha, from Section 6.4.2); (iv) low apple prices, based on 100% processing (£0.2/€0.24 per kg (Lampkin et al. 2017)), to test a wholesale juicing market scenario rather than eating/cooking apples; and (v) the lower and upper estimates of carbon payments for the agroforestry system (based on Section 6.4.3).

6.4 Results

6.4.1 Cereal yields and associations with pests (Question 1)

Grain weight of barley or wheat was 11.4% lower in agroforestry than arable fields, which was statistically significant (t=-2.440, p-value=0.016), but grain weight of organic oats did not significantly differ between agroforestry and arable fields (t=-0.087, p-value=0.931). However, crop type was confounded with year, site and organic management, therefore differences in effects between crop types should be interpreted with caution. Yield of the pooled crop data was 17.2% higher at the centre of the alleys than at 0.5 m from tree rows, but this was not significant (t=1.796, p=0.077).

Cereal yield was significantly negatively associated with weed cover (t=-3.045, p-value=0.003), but was not significantly associated with slug abundance (t=-1.798, p-value=0.076). There was no significant interaction between farming system and either weed cover or slug abundance (Appendix 23).

6.4.2 Apple pollination and yield (Question 2)

Estimated yields of agroforestry-grown apples ranged from 5.677 to 14.835 tonnes per ha of apples (Table 6.2). These values are comparable to expected yields from young organic orchards which typically yield 3 t/ha for years 1-5 and 16 t/ha for years 6-11 (Lampkin et al. 2017). Approximately 70% of Braeburn were of sufficient width for Grade 1 or 2 (Table 6.2), comparing closely with expectations for organic orchards (Lampkin et al. 2017).

Table 6.2. Estimated apple yields (per hectare of apples) at agroforestry sites, calculated based on the number of apples per tree and apple width. Grade 1/2 is based on maximum width of at least 60 mm. Apples per tree and yield could not be obtained from the Norfolk site because the apples were harvested prior to sampling.

Site	Variety	Year of trees	Percentage grade 1/2	Mean apples per tree	Mean estimated weight per apple (g)	Estimated yield (t/ha, all grades)
Nottinghamshire	Braeburn	7	68.7	48.7	104.74	5.677
Nottinghamshire	Bramley	7	100	69.8	191.19	14.835
Oxfordshire	Bramley	6	100	27.6	219.64	6.735
Cambridgeshire	Bramley	11	99	40.8	205.54	9.325
Norfolk	Braeburn	4	70	-	108.80	-
Norfolk	Bramley	4	99	-	184.46	-

Seed set in Bramley apple was significantly higher in four agroforestry sites than five orchard sites (mean 4.05 in agroforestry vs. 2.61 in orchards, z=2.108, p-value=0.035), indicating a higher level of pollination in the agroforestry system. This was however not significant when pesticide application on apples was included as a binary fixed effect (z=-1.110, p-value=0.267), although only one organic orchard site and no agroforestry sites with apple pesticide use were available. Seed set for Braeburn was not significantly different between two agroforestry and four orchard sites (z=-0.286, p-value=0.775), providing no evidence for a difference in pollination service. The value of pollination service in agroforestry-grown apples, relative to orchards, depended on variety and organic management, ranging from 104.08 €/ha compared with conventional Bramley orchards to -28.99 €/ha compared with organic Braeburn (Table 6.3).

Table 6.3. Value of pollination (€/ha/year of agroforestry) in no-spray agroforestry-grown apples, compared with orchards, using seed counts to predict apple weight, grading and fruit set. Positive values represent higher pollination value in agroforestry than orchard systems.

Apple production level	**Value of apple pollination in agroforestry compared with:**			
	Conventional		Organic	
	Bramley orchard	Braeburn orchard†	Bramley orchard*†	Braeburn orchard*†
Low	45.51	30.95	-1.81	-2.23
Average	74.80	50.86	-14.47	-17.84
High	104.08	70.78	-23.52	-28.99

* Only one site was available

† difference in seed counts between agroforestry and orchard systems was not significant

6.4.3 Added value from carbon sequestration / reduced emissions (Question 3)

The net reduction in carbon dioxide emissions in agroforestry compared with equivalent arable systems ranged from 312.9 to 552.4 kg CO_2e/ha/year (Table 6.4). The main contributor to this reduction, and determinant of variation therein, was carbon sequestration by apple trees. Using predicted market prices of carbon over the next 20 years, the equivalent annual value (EAV) of net carbon emission reductions in the agroforestry compared with arable systems ranged from 44.96 to 49.57 €/ha for the lower estimate of fruit tree sequestration, to 65.54 to 70.15 €/ha for the upper sequestration estimate (Table 6.5). Using non-market shadow price of carbon, these figures increased to 53.71 to 59.12 €/ha, and 78.26 to 83.66 €/ha (Table 6.5), for lower and upper sequestration estimates respectively.

Table 6.4. Modelled greenhouse gas (GHG) emission reductions and sequestration in the agroforestry versus equivalent arable systems. Ranges are given for reduction emissions as these depend on the crop stage of the rotation, and the range for fruit tree sequestration represents data from different studies.

System	Production level	Reduction in emissions from crop residues (kg CO_2e/ha/year)	Sequestration from fruit trees (kg CO_2e/ha/ year)	Net change in GHG (kg CO_2e/ha/year)
Conventional	Low	39.2 to 59.4	303.4 to 460.0	342.8 to 519.4
	Average	45.8 to 70.3		349.4 to 530.3
	High	52.3 to 81.9		355.9 to 541.9
Organic	Low	9.3 to 92.4		312.9 to 552.4
	Average	9.9 to 92.4		313.5 to 552.4
	High	1.2 to 92.4		315.3 to 552.4

6.4.4 Gross mixed income of the agroforestry system (Question 4)

Theoretical gross mixed income

Modelling predicted that the agroforestry system was initially at negative cash-flow, arising from establishment costs and the time-lag before apples became productive. By the end of the 20-year simulation however, gross mixed income (GMI), represented by net present value (NPV) and equivalent annual value (EAV), in agroforestry was higher than for the equivalent arable systems in 15 of the 18 modelled scenarios (Fig. 6.1, Table 6.5). Of these 15, NPV in agroforestry exceeded the equivalent arable scenario after seven to 14 years (Table 6.5). The three agroforestry scenarios with lower GMI than arable systems were all organic systems with low apple productivity. In these scenarios, GMI (expressed as EAV) of the agroforestry system remained lower than for the equivalent arable system even without establishment costs.

Table 6.5. Economic performance of agroforestry (AF) compared with equivalent arable systems, under 18 different scenarios of management regime, arable crop productivity level (PL) and apple productivity level (as defined by farm management handbooks). Cumulative gross mixed income is represented by net present value (NPV), whilst EAV is the equivalent annual value for a 20-year system lifespan. All financial values (NPV/EAV) are expressed as €/ha.

Scenario			**Years for AF NPV to exceed arable NPV**	**Arable EAV**	**AF EAV with establish. costs**	**AF EAV without establish. costs**	**Carbon EAV (market price)**	**Carbon EAV (shadow price)**
Inputs	**Arable PL**	**Apple PL**						
Conven-tional	Low	Low	12	97.01	210.35	352.20	46.97 – 67.56	56.02 – 80.57
		Average	9	97.01	475.23	617.07		
		High	7	97.01	740.10	881.95		
	Average	Low	13	315.43	408.68	550.52	48.24 – 68.82	57.54 – 82.08
		Average	9	315.43	673.55	815.40		
		High	7	315.43	938.43	1080.27		
	High	Low	14	539.84	612.45	754.29	49.57 – 70.15	59.12 – 83.66
		Average	9	539.84	877.32	1019.17		
		High	7	539.84	1142.19	1284.04		
Organic	Low	Low	Infinite	10.41	-272.74	-95.85	44.96 – 65.54	53.71 – 78.26
		Average	11	10.41	230.09	406.99		
		High	8	10.41	589.26	766.15		
	Average	Low	Infinite	115.92	-176.94	-0.04	45.41 – 65.99	54.24 – 78.79
		Average	11	115.92	325.90	502.79		
		High	8	115.92	685.06	861.96		
	High	Low	Infinite	270.47	-36.61	140.29	45.50 – 66.58	54.93 – 79.47
		Average	11	270.47	466.22	643.11		
		High	8	270.47	825.39	1002.28		

Modelled GMI based on a case study agroforestry system

Cereal yields at the case study farm were similar between agroforestry and arable fields, and were similar to or higher than those stated in the Organic Farm Management Handbook for a high productivity level organic farm, while apple yields were between low and medium productivity levels (Lampkin et al. 2017). According to 1000 simulations using random samples taken from the empirical data, the EAV of the agroforestry simulations over the 20-year system lifecycle was 10.25 €/ha (8.69 £/ha) higher than the equivalent arable simulations. Cumulative

GMI (expressed as NPV) of the agroforestry system was higher than the arable system within the 20-year lifecycle in 75.7% of cases. In those cases, the agroforestry system was initially at negative cash-flow but NPV exceeded the equivalent arable system after a mean of 17.79 years. This is consistent with the theoretical expectation for an organic farm with high arable productivity and low to average apple productivity (Table 6.5).

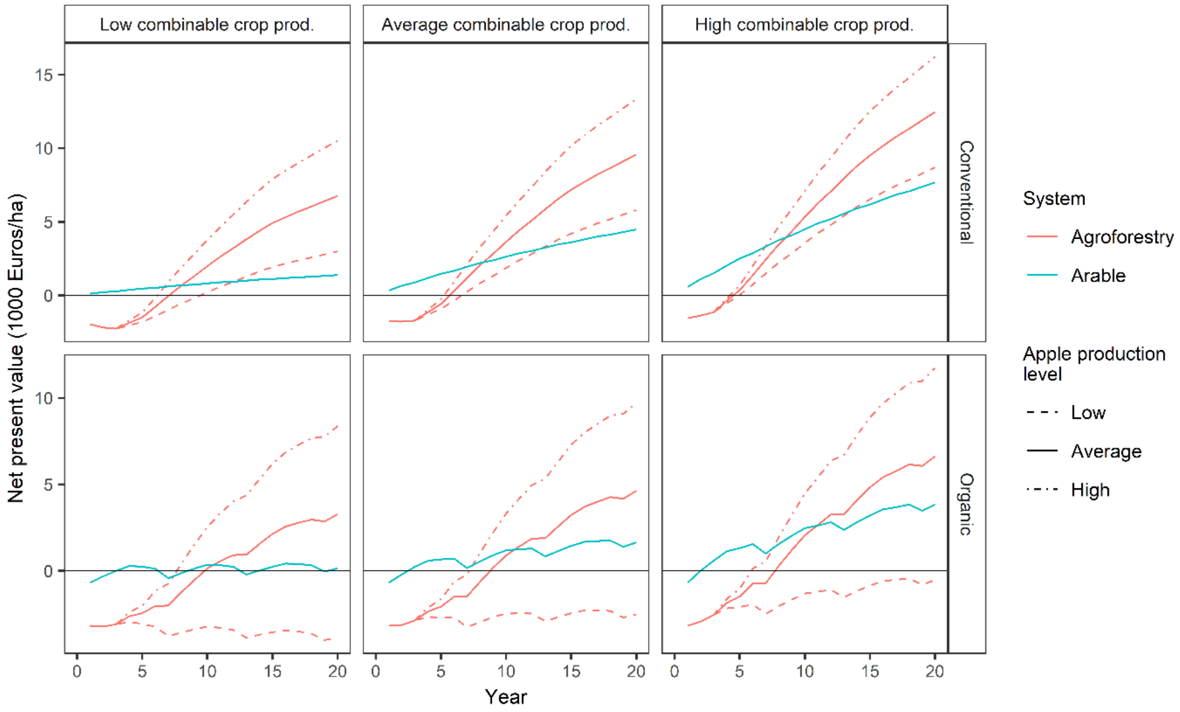


Figure 6.1. Modelled cumulative gross mixed income (expressed as net present value) of agroforestry versus arable systems over a 20-year system lifespan. Each column represents a combinable crop productivity level, whilst the rows represent conventional or organic management.

Sensitivity analysis

Sensitivity analysis of the above case-study simulation identified that apple yield and price were the major factors determining GMI of the agroforestry system (Fig. 6.2). For example, simulations based on the upper estimate of apple yield (14.49 t/ha) increased EAV of the agroforestry system by 61% compared with the baseline scenario where mean apple yield was 4.81 t/ha. Simulations assuming wholesale processing prices for all apples (£0.2/€0.24 per kg) reduced EAV by 36% compared with the baseline assumption of 70% Grade 1 or 2 wholesale apples.

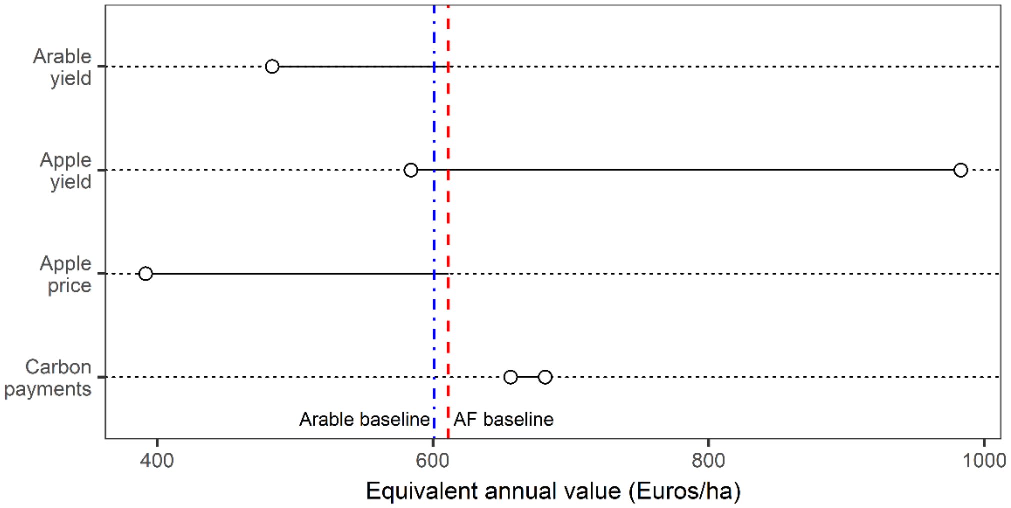


Figure 6.2. Sensitivity analysis to compare alternative scenarios for the agroforestry system. The arable and agroforestry (AF) baseline scenarios are mean equivalent annual values (EAV) from the case study simulation. The points represent mean EAV of agroforestry under the following scenarios, with inputs manipulated in isolation: the arable yield scenario assumes 11.4% reduction in arable yield in the agroforestry system (from Section 6.4.1), the apple yield scenarios represent the minimum yield recorded from the case study farm (4 t/ha, excludes establishment years) and the maximum yield from an agroforestry system (Section 6.4.2), the low apple price scenario assumes a processing price of 0.24 €/kg for all apples (compared with 70% Class 1/2 at 1.06 €/kg for the baseline scenario), and the carbon scenarios represent grant payments for carbon sequestration (Section 6.4.3).

6.5 Discussion

In this study we (i) compared empirical arable and apple yields between agroforestry and monoculture (arable/orchard) systems, (ii) evaluated the costs and benefits of weed/pest pressure, apple pollination, and carbon sequestration in terms of productivity and/or gross mixed income (GMI), and (iii) modelled GMI of the agroforestry versus arable systems. We found 11% lower wheat/barley yields in the agroforestry than arable system, but no significant effect for oat yield, while there were significant negative associations between yield and weed cover. Apple yields in the agroforestry system were highly variable among sites and varieties, but were consistent with expected yields in comparable orchards. Apple pollination level, as indicated by seed set, was significantly higher in agroforestry-grown Bramley apples than conventional orchards, but there was no significant difference after accounting for pesticide use, or for Braeburn apples. Cumulative GMI of the agroforestry system was predicted to be higher than that of an equivalent arable system within a 20-year lifespan, except in low apple production organic systems. Financial modelling of a case study system, using empirical data, was consistent with theoretical predictions. A sensitivity analysis demonstrated that apple yield and price were the major determinants of GMI of the agroforestry system, and were capable of more than compensating for an 11% reduction in arable yield. Carbon sequestration and reductions in emissions added further value to the agroforestry system.

6.5.1 Cereal productivity

Our finding of lower wheat/barley yields in the agroforestry compared with arable systems is consistent with short-term yield reductions in other diversified farming systems (reviewed in Rosa-Schleich et al. 2019). The 11% yield reduction compares favourably to the 10-26% reductions for barley and 11-15% reductions for wheat in a timber agroforestry system with 12 m wide alleys (García de Jalón et al. 2017; Giannitsopoulos et al. 2020). Furthermore, in that timber system, arable cropping was predicted to be unprofitable after 5 to 13 years depending on alley width (Burgess et al. 2003), whereas continuous arable cropping appears to be financially viable in the apple-arable agroforestry system, albeit longer-term yield monitoring is needed. Our yield effects however compare less favourably to the reported 16% increase in wheat yield in a short-rotation coppice system with 48 m wide alleys (Kanzler et al. 2019), while another study found similar yields between short-rotation coppice systems with 48 and 96 m wide alleys, and arable control fields (Swieter et al. 2019). Although the effects of farming system on yield of different crop types was confounded with site and should be interpreted with caution, we found comparable oat yields between the agroforestry and arable systems, possibly because oats are more competitive with weeds and resistant to slug damage than wheat or barley (Douglas & Tooker 2012; Seavers & Wright 1999).

We found a negative relationship between cereal yields and proximity to tree rows, although the results were not statistically significant (p-value=0.77). Nevertheless, alley width is likely to be an important factor when comparing yields between agroforestry and arable systems (Burgess et al. 2003). For example, according to a meta-regression, tree rows and hedgerows reduce yields of adjacent crops, relative to arable controls, up to a distance into the crop alley of 1.64 times the tree height (Van Vooren et al. 2016), but have positive or negligible effects thereafter. This translates to approximately half of the crop alley in an apple-arable agroforestry system with 24 m wide alleys and MM106 rootstocks, where the trees reach approximately 4 m height, which are typical choices for modern agroforestry systems.

Competition between trees and arable crops for resources such as water, light and nutrients has been cited as the major cause of arable yield reductions in agroforestry systems (Jose et al. 2004), although cultivar selection programs have potential to mitigate this (Arenas-Corraliza et al. 2021). Our finding of negative associations between weed cover and yield suggests that weed competition could also be a factor in organic agroforestry systems, although we cannot demonstrate any causal relationship. Previous studies have shown that weed cover in agroforestry versus arable systems varies among sites, possibly depending on the response traits of the dominant weed species (Boinot et al. 2019a; Staton et al. 2021b), suggesting that this potential cause of yield reduction may only apply to sites with problematic creeping, perennial weeds. Similarly, slug abundance has previously been linked to pea crop damage in agroforestry crop alleys (Griffiths et al. 1998). We found no significant evidence for this based on spring counts, although autumn and winter slug abundance may be of more relevance for winter-sown crops.

Despite the short-term negative effects on wheat/barley yield, yield stability is typically higher in diversified farming systems, including intercropping of annual crops, compared with non-diversified systems (Raseduzzaman & Jensen 2017; Rosa-Schleich et al. 2019), while proximity to semi-natural habitats improves yield resistance to extreme weather events (Redhead et al. 2020). Agroforestry systems could improve yield stability and climate resilience by moderating the impacts of extreme weather events, such as drought and high winds (Arenas-Corraliza et al. 2018; Kanzler et al. 2019), and in the longer-term, protection from soil erosion (Tsonkova et al. 2012; Varah et al. 2013). Natural enemy activity has also been postulated as a probable mechanism for higher yield stability with proximity to semi-natural habitat (Redhead et al. 2020), and agroforestry systems increase the functional trait diversity of natural enemies compared with arable monocultures (Staton et al. 2021b).

6.5.2 Apple productivity and pollination

We found that apple yields in the agroforestry system strongly varied among sites, even for the same variety. Possible explanations for this variation are differences in site conditions such as soil type, management (e.g. pruning), alternate bearing (natural yield fluctuations between years), and tree age, which varied from 6 to 11 years, the youngest of which had only just entered full production. Productivity data from this novel agroforestry system are scarce, although Smith et al. (2016) also found substantial variation in apple yields; depending on variety and year, yields varied from 0.25 to 15.18 t/ha (of apple trees) for the 5-6 year old Cambridgeshire system also used in our study, and 15.7 to 19.25 t/ha for a 18-19 year old system which used MM111 rootstocks. At the Cambridgeshire site, Bramley yields of 0.35 and 3.71 t/ha were reported in 2014 and 2015 respectively, compared with our finding of 9.33 t/ha in 2020. The existing data tentatively suggests that fruit trees in agroforestry settings could take longer than expected to enter full production, possibly because the understorey vegetation competes for resources (Granatstein & Sanchez 2009) and because of the more exposed conditions.

Pollination levels in Bramley, represented by seed set, were significantly higher in the agroforestry system than in conventional orchards, but preliminary findings from one organic orchard suggest similar levels to the agroforestry sites. Furthermore, we found no significant difference between agroforestry and orchard systems for Braeburn seedset, suggesting that the comparison between agroforestry and orchard systems is complex and moderated by other factors such as variety and pest management. Nevertheless, our findings suggest that the more exposed conditions and lower densities of apples trees in agroforestry compared with orchard systems does not substantially reduce seed set.

6.5.3 Carbon sequestration

We estimated a reduction in greenhouse gas emissions in the agroforestry compared with arable systems of 312.9 to 552.4 kg CO_2e/ha/year, the majority of this (83 to 97%) being attributable to sequestration by trees. This is at the lower end of the predicted range of 366 kg to 11 t CO_2e/ha/year for tree sequestration over a 60-year simulation of European agroforestry systems (Palma et al. 2007a). While sequestration will inevitably be lower than fast-growing timber agroforestry systems (e.g. Giannitsopoulos et al. 2020), our results suggest that the apple-arable agroforestry system can make a meaningful contribution to climate change mitigation in agriculture, which we value at between 44.96 and 70.15 €/ha per year (equivalent to net present value (NPV) of 639 to 997 €/ha) using predicted market carbon prices, or 53.71 and 83.66 €/ha per year (NPV of 763 to 1189 €/ha) for non-market shadow price. Given the reported establishment costs of 1357 €/ha of the agroforestry system (Newman et al. 2018), an upfront carbon payment would cover 47% to 73% of these costs using market prices, or 56% to 88% using shadow prices.

6.5.4 Farm income

Cumulative gross mixed income (GMI) of the agroforestry system was consistently predicted to be higher than the equivalent arable system within a 20-year system lifespan, with the exception of organic systems with low apple productivity. Apple productivity and price were the most important factors determining GMI of the agroforestry system, and were capable of substantially outweighing an 11% reduction in cereal yield. For example, by assuming apple yields were consistently at the maximum recorded in the study, equivalent annual value (EAV) of GMI increased by €349 compared with the baseline agroforestry scenario, while the difference between 70% Class 1 or 2 and 100% processing wholesale prices represented €233 EAV. These compare to a loss of €147 EAV resulting from an 11.4 % reduction in arable yields in the agroforestry system. These figures demonstrate the importance of proper management and protection (i.e. staking and shelterbelts) of apple trees, availability of sufficient labour, and identification of markets, particularly given that this agroforestry system is typically implemented by arable farmers without prior experience of apple production. In addition, further research is needed to identify which apple varieties are best suited to agroforestry conditions (Smith et al. 2016).

The expected time taken for cumulative GMI (expressed as NPV) of the agroforestry system to exceed arable was 7 to 14 years in the theoretical systems (for the 15 of 18 cases where the GMI of the agroforestry system exceeded that of the equivalent arable system), depending on organic management and productivity level. This increased to 18 years in the case study system, because of relatively low apple yields and high arable yields. Nevertheless, this still compares favourably to timber agroforestry systems, where a return on investment is not expected until at least 20 years (Graves et al. 2007; Van Vooren et al. 2016), and is dependent on timber prices, grant payments and discount rates (e.g. Giannitsopoulos et al. 2020; Palma et al. 2007b; Toor et al. 2012).

The adoption of agroforestry systems is mainly constrained by management and labour complexity factors (García de Jalón et al. 2018). Although our results suggest that agroforestry can increase GMI relative to arable systems, in order to effectively promote agroforestry systems, farmers need to perceive that the benefits such as long-term GMI exceed the perceived drawbacks. A wider valuation of non-marketable ecosystem services could therefore help to promote these systems.

6.5.5 Other ecosystem services

Previous studies have demonstrated the potential for agroforestry systems to provide other ecosystem services. For example, the value of reduced soil erosion by water, and balances of nitrogen and phosphorous, have been estimated at 5, 8 and 18 €/ha/yr respectively in a UK silvoarable system compared with an arable control (Giannitsopoulos et al. 2020). In that case study, the arable crop alleys were put to grass fallow after 14 years of the 30-year system lifespan, therefore the value of these services in our study system is likely to be less, assuming continuous arable cropping. Another important ecosystem service in some regions is soil protection from wind, which to our knowledge has not yet been assessed in agroforestry systems, and would be strongly spatially dependent. A holistic monetary quantification of the ecosystem services provided by agroforestry, for example extended accounting systems such as the Agroforestry Accounting System, would help to inform the design of public policies to promote the adoption of these systems (Campos et al. 2020; Giannitsopoulos et al. 2020).

6.5.6 Constraints and research needs

Our results are based on arable and apple yield data collected over two years from five agroforestry sites, the most established being 11 years. As such they would benefit from further, long-term replicated studies and validation from other sites and from more established systems. Long-term yield data is important to investigate biodiversity benefits, yield stability and implications for food security. In addition, our assessment of pest and weed impacts on crop yields are based on associations, rather than demonstrating causal relationships. Further research is needed to quantify the impacts of changes in pest abundance on chemical control costs (Johnson et al. 2020). Our comparison of apple pollination is constrained by confounding factors, particularly organic management, tree age and landscape context, and would benefit from further investigation to disentangle these factors.

Land equivalent ratios (LERs) are a common method for comparing productivity between agroforestry systems and equivalent monocultures. LER calculates the area of monoculture required to achieve the same level of productivity of one unit of polyculture, and was originally devised for intercropped annual crops (Mead & Willey 1980). We did not calculate LER in this study because: (i) we did not have empirical or robust modelled yield data for the lifespan of the system, particularly for apples, (ii) we did not have comparable monoculture apple (orchard) yield data, (iii) as discussed by Newman et al. (2018), the method for LER calculations in previous studies of agroforestry systems is inconsistent, because studies variously use yield per area of the crop component or per area of agroforestry. This leads to problems in comparing LER calculations from previous studies. A synthesis of previous LER agroforestry studies using a standardised methodology would help overcome this problem, and the data we present in this study could potentially be used in any such future synthesis, notwithstanding the above constraints.

6.5.7 Conclusions and implications

There appear to be trade-offs from higher biodiversity in agroforestry systems; weed cover was negatively associated with arable yields, but Bramley apple seed set, which indicates pollination level, was higher in agroforestry than conventional orchard systems. Organic management was a complicating factor however, and requires further investigation. In addition, further research is needed to investigate yield stability in agroforestry systems arising from the higher functional diversity of natural enemies.

Apple yield and price were the major determinants of gross mixed income (GMI) of the agroforestry system, and were capable of compensating for an 11% wheat/barley yield reduction in the long-term. However, the time-lag for the GMI of the agroforestry system to exceed that of the equivalent arable system was substantial (at least 7 years), while labour and expertise requirements represent additional barriers. Hence, policy support in the form of establishment grants would help to promote these systems. This could be partially met by up-front payments for carbon sequestration.

6.6 Data availability

The data presented in this chapter are available from Mendeley Data at https://doi.org/10.17632/rjf86nv3n6.1.

7. Thesis discussion

This thesis aimed to improve our understanding of how temperate apple-arable agroforestry systems affect functional biodiversity, associated ecosystem services (natural pest control and pollination), and farm income, relative to monoculture arable systems. This chapter discusses the key findings of the thesis and how they contribute to this aim, followed by a wider overview of the potential for agroforestry as a diversified farming system. Possible future research directions are identified, followed by a discussion of the research findings in the form of non-technical answers to practical questions.

7.1 Key findings

The findings of this thesis can be synthesised into four key findings as follows:

1. plant and invertebrate biodiversity was higher in agroforestry than arable systems (relates to objectives 1 and 2 of the Introduction chapter (Section 1.8));
2. agroforestry systems led to changes in the composition of plant and invertebrate communities, which can be explained in terms of their functional traits (relates to objectives 1 and 2);
3. tree row understorey management was a key confounding variable of agroforestry effects on invertebrate biodiversity (relates to objective 3);
4. agroforestry systems led to trade-offs in ecosystem services, productivity, and farm income (relates to objective 4).

Each of these key findings is discussed individually below, while Figure 1.2 from the Introduction is updated in Figure 7.1 to demonstrate the main findings of the thesis.

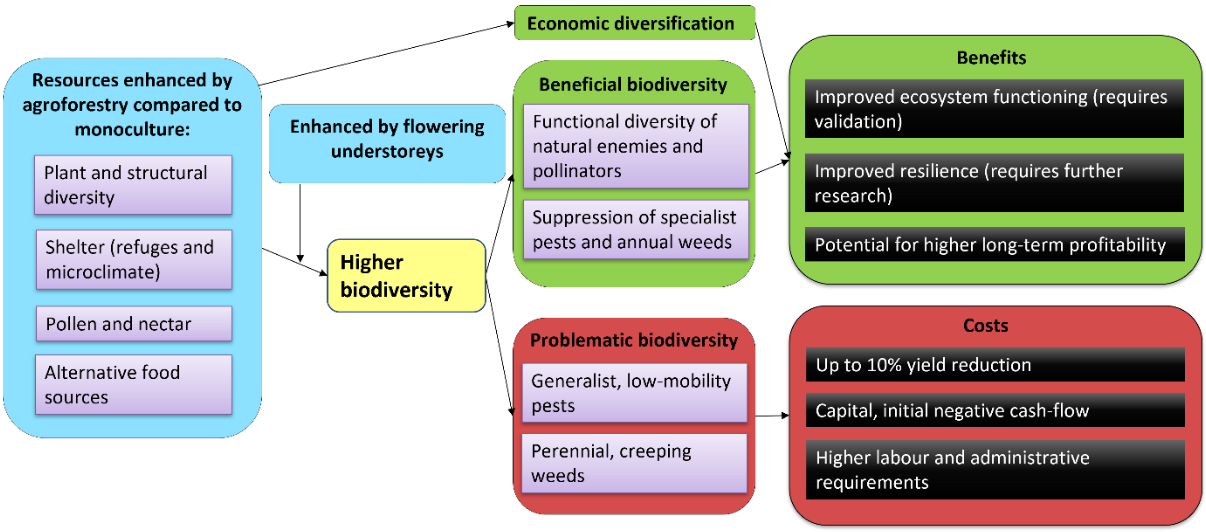


Figure 7.1. Flow-chart summarising the main findings of the thesis, outlining how agroforestry systems enhance biodiversity which leads to community changes and financial costs and benefits. The figure is adapted from Figure 1.2 in the Introduction chapter; the left-hand box is unchanged but other boxes are adapted and refined according to the thesis findings.

Key finding 1: plant and invertebrate biodiversity was higher in agroforestry than arable systems

The results presented in Chapters 3 and 4 across three agroforestry sites with paired arable controls support previous studies which found higher biodiversity in agroforestry than monoculture systems, as discussed in Chapter 2 (Torralba et al. 2016; Tsonkova et al. 2012; Varah et al. 2013). However, Chapter 3 is the first study to identify stronger effects on taxonomic richness and diversity at lower trophic levels in agroforestry systems, i.e. the increase in diversity was higher for plants than for invertebrate herbivores, which is turn was higher than invertebrate natural enemies. This effect was observed by comparing agroforestry crop alleys with arable fields, demonstrating a spill-over effect from tree rows into crop alleys. We also found strong effects on bee richness and diversity, supported by previous evidence (Varah et al. 2020), but not for hoverflies, in Chapter 4. These beneficial effects on biodiversity can be explained in terms of reduced disturbance and higher niche diversity in agroforestry systems than monocultures (Stamps & Linit 1998).

Ecological intensification of agriculture, and the similar concept of diversified farming systems, have been proposed as possible solutions to halt and reverse biodiversity losses from agricultural practices (Habel et al. 2019; Kehoe et al. 2017; Kremen et al. 2012). The findings in this thesis demonstrate that the integration of trees into arable systems is a viable strategy to restore biodiversity, supporting previous recommendations which advocate the implementation of agroforestry systems for biodiversity (Dicks et al. 2016; Torralba et al. 2016; Udawatta et al. 2019). However, the benefits of agroforestry systems to biodiversity are not equal across all species, as discussed in the next key finding.

Key finding 2: changes in plant and invertebrate communities explained by functional traits

The review and meta-analysis in Chapter 2 concluded that invertebrate natural enemies were significantly more abundant, and arthropod pests significantly less so, in silvoarable versus arable systems. However, effect sizes were highly variable, and the effect of farming system on all invertebrate pests (that is, including molluscan pests) was not significant, suggesting that the effect of farming system could be taxon-dependent. The new data presented in Chapter 3 supported this hypothesis, with three invertebrate taxa significantly suppressed in agroforestry versus arable systems, while one invertebrate taxon (slugs) was significantly more abundant in the agroforestry systems. Furthermore, in Chapter 4, species richness and diversity of bees responded significantly to farming system, but hoverflies did not.

These findings strongly suggest that the implementation of agroforestry systems leads to a change in communities of plants and invertebrates. This is further supported by recent studies comparing plant and invertebrate communities in tree rows versus crop alleys within agroforestry systems (Boinot et al. 2019a, b), while differing responses of pest species has been observed in relation to flower margins (Eggenschwiler et al. 2013; Tschumi et al. 2015). Together, this evidence would suggest that simply measuring the overall abundance of functional groups (e.g. natural enemies, pollinators) leads to inconsistent results (Karp et al. 2018; Lichtenberg et al. 2017) because the implementation of agroforestry systems (and possibly other diversified farming systems) changes the community structure of functional biodiversity rather than leading to a universal and consistent increase or decrease in abundance across the functional group.

This change in community composition can be understood in terms of functional trait responses to farming system (Brousseau et al. 2018; Wong et al. 2019). Chapter 3 revealed how the plant and invertebrate community responded to agroforestry versus arable systems: agroforestry systems supported a more perennial, creeping plant community, and a more diet-specialist or granivorous, less mobile invertebrate community, compared with arable systems. This can be explained in terms of disturbance and year-round habitat availability in tree rows. Furthermore, Chapter 4 extended this trait-based analysis to reveal changes in bee functional diversity between farming systems through niche complementarity, which reflected functional diversity of floral resources in agroforestry tree rows.

These trait-based analyses led to an understanding of how functional biodiversity responds to farming system through functional trait identity and/or functional diversity, which in turns leads to changes to ecosystem functioning (e.g. Garibaldi et al. 2015; Greenop et al. 2018; Woodcock et al. 2019). For example, pest management in agroforestry systems should focus on control of slugs and perennial weeds, whilst crop pollination is likely to be greatest for crops pollinated by smaller bee species or those with long tongues (Garibaldi et al. 2015; Hutchinson et al. 2021). The trait-based approaches also reveal how management can maximise the benefits of agroforestry systems to functional biodiversity, for example by enhancing floral class diversity which in turn structures pollinator functional diversity, as discussed in Chapter 4.

Key finding 3: tree row understorey management was a key confounding variable

Although trait-based approaches can explain much of the variation in biodiversity effects of farming system among sites (e.g. Torralba et al. 2016), a considerable degree of unexplained heterogeneity remains. For example, in Chapter 3, the effect of farming system on the abundance of individual pest taxa, which in some cases were at the species level, varied substantially among sites. This could be explained by numerous potential confounding factors such as system design, farm management, and landscape context, as discussed in Chapter 2.

In Chapter 5, we manipulated one of those factors in isolation, namely understorey management, and found that this was a key determinant of ground-based invertebrate diversity, natural enemy abundance and aphid colonies in apple trees, and pollinator visitation to apple flowers. Furthermore, this factor interacted with season. Although this is from one case-study farm replicated across five blocks, the findings were consistent with other studies comparing spiders and slugs adjacent to bare versus vegetated understoreys in agroforestry systems (Burgess et al. 2003), and of flower strips in agro-ecosystems (Albrecht et al. 2020; Ganser et al. 2019, 2020). Furthermore, the findings of Chapter 4 suggest that increases in pollinator functional diversity in agroforestry systems was driven by the plant community in the tree row understoreys, indicating that understorey management could be an important driver of crop pollination service.

Key finding 4: agroforestry systems led to trade-offs in ecosystem services, productivity, and farm income

The literature review and meta-analysis in Chapter 2 identified that most studies of biodiversity in agroforestry systems measured abundances, with only four studies also recording some measure of crop damage or yield. As such, Chapter 2 identified a need to assess the productivity and financial costs and benefits of agroforestry systems, which has similarly been advocated for diversified farming systems more broadly (Chaplin-Kramer et al. 2019; Kleijn et al. 2019).

One potential disservice in agroforestry systems is an increase in weed cover, as revealed in Chapter 3, albeit with substantial variation among sites and a shift towards a more perennial and creeping community. Furthermore, Chapter 6 reported a negative association between weed cover and cereal yields in both agroforestry and arable systems. Therefore, Chapters 3 and 6 suggest that pressure from perennial, creeping weeds represents a risk to productivity, and therefore farm income, in agroforestry systems. On the other hand, advantages of biodiversity in agroforestry systems for productivity include the potential for higher apple pollination levels in agroforestry compared with orchard systems (Chapter 6), and higher functional trait diversity of natural enemies and pollinators in agroforestry systems versus arable monocultures (Chapters 3 and 4), which could indicate improved ecosystem functioning in terms of pest suppression and crop pollination (Greenop et al. 2018; Martins et al. 2015; Woodcock et al. 2019). Importantly for farmers, apple yield and price were predicted to be more important determinants of farm income than arable yield (Chapter 6), therefore, a small increase in weed pressure can be offset if apple production is high and/or a good market for apples is identified. These findings were based on a modelling approach, albeit based on empirical data, and would therefore benefit from further empirical validation.

The reduction in cereal productivity in agroforestry compared with arable systems was similar to those reported from other diversified farming systems, as discussed in Chapter 6. This suggests that the productivity of agroforestry systems is typical of a diversified farming system, but in order to meet projected global food demands, other strategies including diet adaptation, waste reduction, and improved efficiencies are required (Conijn et al. 2018; Davis et al. 2016).

7.2 The potential for agroforestry as a diversified farming system

Diversified farming systems involve the intentional integration of functional biodiversity at multiple spatial or temporal scales, through traditional and/or scientific knowledge, and include practices such as intercropping, crop rotations, hedgerows, and semi-natural habitats (Kremen et al. 2012). Therefore, diversified farming systems can be implemented at the plot, field, and landscape scales. In this thesis, we focus on smaller-scale agroforestry intercropping systems (Fig. 7.2). The functional biodiversity promoted by diversified farming systems, both intentionally and unintentionally, leads to improved ecosystem service delivery, of which the focus of this thesis is on pest control and pollination (Fig. 7.2).

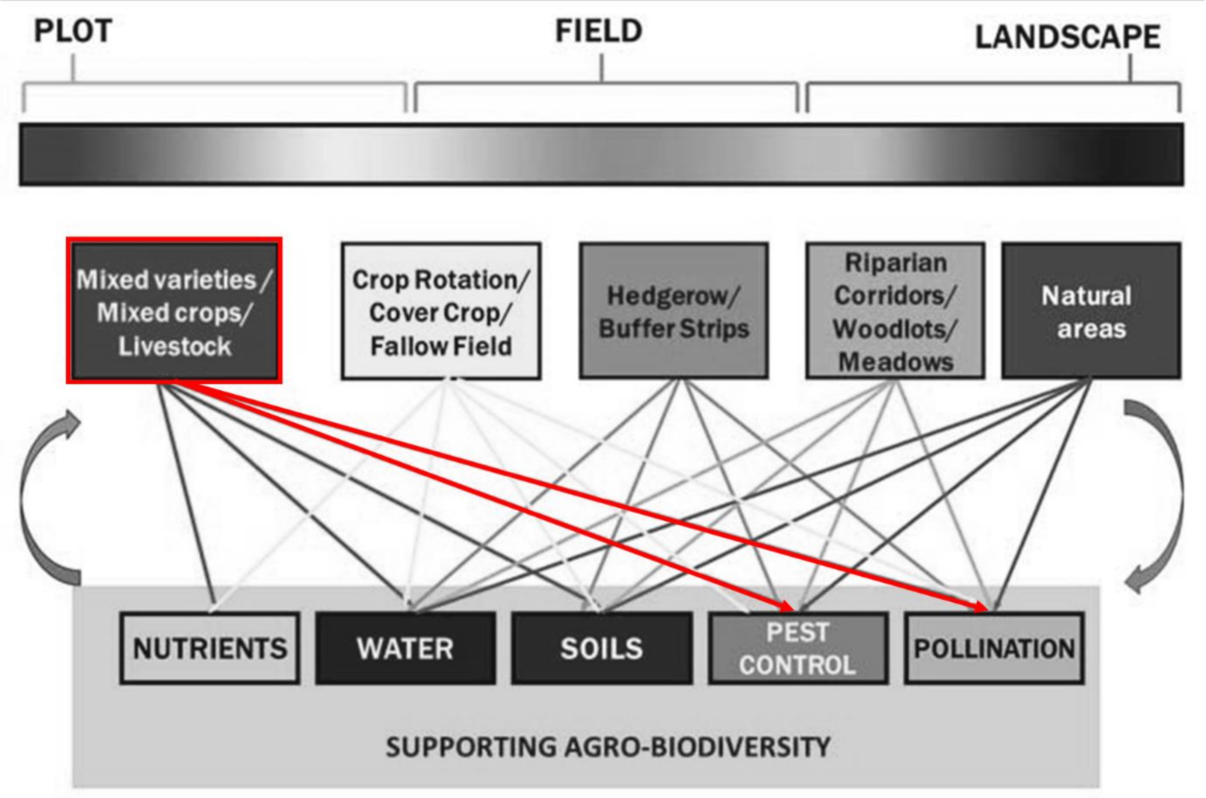


Figure 7.2. The contribution of the research presented in this thesis in the wider context of diversified farming systems (from Kremen et al. 2012). This research focusses on smaller-scale mixed cropping (trees and arable) systems, and their effects on natural pest control (in Chapters 3 and 5) and pollination (Chapters 4 and 5) ecosystem services and their supporting agro-biodiversity.

In a broader context of ecosystem services, agroforestry systems appear to be particularly beneficial for reducing soil erosion and carbon sequestration (Jose 2009; Smith et al. 2013a; Torralba et al. 2016), which are perceived as positive aspects by stakeholders (García de Jalón et al. 2018). However, the need for these ecosystem services, such as soil protection, is not equal across all landscapes. In addition, the findings in this thesis suggest that it is over-simplistic to conclude that pest and weed pressure, and farm income, universally increases or decreases in silvoarable versus arable systems. Instead, the results are more nuanced, and any benefits or disservices will vary according to site context such as landscape composition.

Together, this supports the notion that agroforestry systems are not a ‘one size fits all’ solution to agricultural sustainability, but should be targeted to regions where the benefits of agroforestry systems match local environmental pressures (Kay et al. 2019b). For example, approximately 40% of arable land in Europe was estimated to be suitable for both productive tree growth and at risk of soil erosion, nitrate leaching, and/or impoverished landscape diversity (Reisner et al. 2007). In some regions, for example areas where tree growth is not expected to be productive or with differing environmental pressures, other diversified farming systems might be more appropriate. This targeted approach is extended in Table 7.1 below, with a focus on functional biodiversity.

7.3 Future research directions

The findings presented in this thesis open up a number of avenues for further research. These include more detailed studies of pest control and pollination, investigation of the main drivers and confounding variables of biodiversity in agroforestry systems, a more holistic understanding of ecosystem services in agroforestry systems, and extension of the methods applied in this thesis to wider spatial and temporal scales.

Pest control and pollination: measuring ecosystem functions and services

As identified in Chapter 2 and other reviews of functional invertebrates in agro-ecosystems (Ari Noriega et al. 2018; Johnson et al. 2020), there is a clear need for studies to go beyond species abundance counts and to measure ecosystem functions and services, for example predation rates of sentinel prey, exclusion experiments, crop damage assessments, and crop pollination measures (Chisholm et al. 2014) (Fig. 7.3). Sentinel prey, such as live or dead prey items, artificial prey, and weed seeds, are increasingly used to infer predation rates (Lövei & Ferrante 2017).

Table 7.1. A proposed framework for the targeted implementation of agroforestry systems to maximise ecosystem services and minimise ecosystem disservices.

Favourable conditions for agroforestry	Explanation	Confidence and future research needs
Soil erosion and/or nutrient loss seen as a major problem, e.g. sloped or exposed land	Agroforestry systems have consistently strong effects on reducing soil erosion.	High, sample size of 57 in meta-analysis (Torralba et al. 2016).
Need for carbon sequestration, e.g. national political targets, or individual farm strategies and objectives	A key advantage of agroforestry over other diversified farming systems is its carbon sequestration in woody biomass, the extent of which depends on the tree crop (see Chapter 6 discussion).	High in terms of woody biomass, but the contribution of in-field trees to soil carbon stocks over time requires further research.
Organic farm management	Recent evidence suggests that tree rows function as a source of biodiversity in organic systems, but could be a sink in conventional systems (Boinot et al. 2020).	Moderate, requires testing in other landscapes and climates.
Moderate or low landscape complexity	The benefits of habitat diversification to biodiversity are greatest in landscapes with low to moderate complexity, but could be masked in complex landscapes (Jonsson et al. 2015; Tscharntke et al. 2005).	High, but requires further testing specifically for agroforestry systems.
Free-draining soils	Of all invertebrate pests, slugs appear to pose the greatest risk of crop damage in agroforestry systems (Chapters 2 and 3), possibly because of the more stabilised soil moisture (Boinot et al. 2019b; Kanzler et al. 2019). Soils which are more prone to drying are less suitable for slug foraging (Young & Port 1991) and slugs were almost absent from the agroforestry system on peaty soils in this thesis.	Moderate, strong theoretical basis but requires more empirical evidence.
Local market opportunities for tree product	Chapter 6 identified that the price for the tree product (e.g. apples) is critical for the financial viability of agroforestry systems, which is supported by previous economic modelling studies of other agroforestry systems (see Chapter 6).	High
Suitable conditions for tree production	Similarly, yield of the tree product (e.g. apples or timber) is a critical factor determining the financial viability of agroforestry systems, as identified and discussed in Chapter 6.	High

This project initially aimed to include measures of predation and pollination, and field experiments were conducted to measure predation rates of sentinel frozen maggots, live aphids, and weed seeds (Lövei & Ferrante 2017; McHugh et al. 2020), and pollination of California poppy phytometers (Varah et al. 2020). These experiments proved to be problematic, because of the highly unpredictable and variable rates of predation, coupled with the practical difficulties of monitoring distant field sites. As such, there was insufficient replication of meaningful data to draw any conclusions, but this is worthy of future research, which should use a range of sentinel prey types because of their differing predation rates (Greenop et al. 2019; McHugh et al. 2020; Nagy et al. 2020).

Another important avenue of research is to investigate crop damage by pests and disease in agroforestry systems (Johnson et al. 2020). For example, previous research across two sites suggests that levels of apple scab can be lower in agroforestry versus orchard systems, but there was some indication that this might depend on the arrangement of apple varieties (Smith et al. 2016). In addition, a recent study demonstrated higher pollination levels of phytometers in agroforestry systems than monocultures of cereals or pasture (Varah et al. 2020). To advance our understanding of pollination in agroforestry systems, measures of pollination of field-scale crops such as oilseed rape or field beans are needed, given that the extent of mass-flowering crops affects pollinator distribution (Diekötter et al. 2010; Shaw et al. 2020).

Chapters 3 and 4 identified higher functional trait diversity of natural enemies and pollinators in agroforestry compared with arable systems. The long-term value of taxonomic and functional trait diversity of beneficial fauna requires further investigation, particularly in terms of the potential benefits on the resilience and stability of ecosystem services in the context of a changing climate (Jonsson et al. 2017; Oliver et al. 2015) and the risk of pest outbreaks (Chaplin-Kramer et al. 2019).

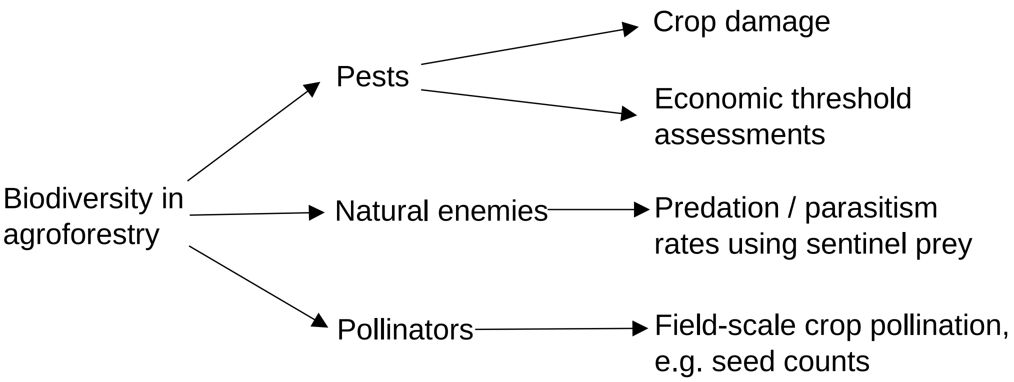


Figure 7.3. Framework for conducting future research of natural pest control and pollination in agroforestry systems, which is similarly applicable to other diversified farming systems.

System age and other factors determining functional biodiversity in agroforestry systems

As discussed in Chapter 2, there are numerous interacting factors which explain the heterogenous responses of biodiversity to farming system (agroforestry versus arable). The findings in this thesis also tentatively suggest that age of the agroforestry system could be an important variable influencing biodiversity. For example, in Chapter 3, the taxonomic richness and diversity of plants, invertebrate herbivores and invertebrate natural enemies in agroforestry systems relative to arable controls were all greatest in the longest-established site. Similarly, Chapter 4 revealed that the effect of farming system on bee functional richness and functional dispersion was greatest at the longest-established site. However, the data presented in those chapters was limited to three sites, mainly because of the scarcity of established silvoarable agroforestry systems, with paired arable control fields, in the UK.

As such, the effect of system age could not be rigorously tested, and it is possible that other confounding factors such as landscape context or size of the system could explain these effects. For example, the longest-established agroforestry system was also situated in the most simplified, agriculturally-intensive landscape, which could have amplified the biodiversity benefits of the agroforestry system compared with sites in more complex landscapes (Jonsson et al. 2015; Tscharntke et al. 2012). Establishment age of the three sites was also correlated with size of the agroforestry system, with the longest-established site comprising the largest agroforestry system (Appendix 3).In addition, two of the three sites were organically managed, which influences biodiversity in agroforestry systems (Boinot et al. 2020). These two interacting factors could account for much of the heterogeneity in effect sizes among sites (Ricci et al. 2019; Tscharntke et al. 2012).

The importance of establishment age of an agroforestry system on biodiversity and associated ecosystem services could be tested in two ways. Firstly, a meta-analysis could include system age as a variable. Secondly, a study at a larger temporal and/or spatial scale could more rigorously test this hypothesis, either by monitoring a low number of sites for a long duration, to observe biodiversity changes over successive years, or by sampling from a high number of sites of different ages. A key unknown question is the pattern of biodiversity changes over time in agroforestry systems. After a new agroforestry system is planted, biodiversity might incrementally increase over a period of time as species colonise, but in other systems the process of colonisation appears to rapid and quickly saturates (Albrecht et al. 2020; Pywell et al. 2005). This is likely to be dependent on contextual factors such as landscape composition and connectivity from which source populations can colonise (Tscharntke et al. 2012). A better understanding of this process would help to maximise biodiversity benefits of agroforestry systems, for example if they could be targeted in landscapes where existing features such as hedgerows will facilitate rapid colonisation of functional biodiversity.

Multiple ecosystem services in agroforestry systems

Agroforestry research in general would benefit from multi-disciplinary, collaborative and large-scale studies to evaluate synergies and trade-offs of multiple ecosystem services across agroforestry systems, in tandem with social and behavioural investigations. Although evidence for multiple ecosystem service benefits is continuing to emerge through novel modelling approaches (Rolo et al. 2021), most empirical studies, including this study, focus on a single or narrow range of ecosystem services at a small number of sites, which constrains any comparative assessment of the relative importance of different ecosystem services. By contrast, modelling studies are able to account for a wider range of ecosystem services, but are limited by a lack of empirical verification. For example, a verified modelled evaluation of the importance of in-field trees to water retention, soil erosion, nutrient retention, wind protection, moderation of microclimates, and crop production, would lead to a more holistic and robust understanding of how agroforestry systems can improve multiple ecosystem services, compared with disservices such as tree-crop competition for light and water (Jose et al. 2008). Furthermore, the adoption of agroforestry systems ultimately depends on the perceptions and behaviour of agricultural land owners and tenants, therefore, studies should be aligned with these real-world obstacles (Chaplin-Kramer et al. 2019) together with cultural ecosystem services (Rolo et al. 2021).

A broader perspective: diversified farming systems across spatial and temporal scales

The methods applied in this thesis could be applied across wider spatial and temporal scales, for example, to investigate the role of hedgerows, fallow fields, and semi-natural habitat elements in contributing to gamma diversity and functional diversity, stability through dispersal and recolonisation, and resilience through redundancy. For example, although Chapter 4 finds no consistent evidence for rare species contributing to functional dispersion and therefore ecosystem functioning, rare species might become increasingly important at larger spatial and temporal scales (Brittain et al. 2013; Kühsel & Blüthgen 2015; Winfree et al. 2018).

7.4 Recommendations for agroforestry practitioners

The results of this thesis have practical implications for agroforestry farmers. This section is broken down into key applied questions which are addressed by the findings in this thesis, and the degree of confidence in answering those questions.

Will planting trees on a farm benefit or worsen invertebrate pest and weed pressure?

As discussed in the second key finding above, this thesis presents evidence that agroforestry systems lead to a change in pest and weed pressure, which can be understood and predicted in terms of traits. For example, perennial and creeping weeds such as creeping thistle are likely to be more of a challenge in agroforestry than arable systems, while annual seed-spreading weeds such as black-grass are not expected to be more prevalent in agroforestry. Similarly, less mobile, generalist-diet pests such as slugs are predicted to be a challenge in agroforestry systems, but not specialist mobile pests such as pollen beetles or cabbage stem flea beetle. These findings were broadly consistent across our three sites, and are partially supported by other studies (Boinot et al. 2019a; Burgess et al. 2003; Griffiths et al. 1998).

How to manage weeds and invertebrate pests in agroforestry systems?

Perennial weeds and generalist, low-mobility pests such as slugs appear to be the main risk in agroforestry systems. In the arable crop alleys, tillage regimes and crop rotation could be adjusted to reduce competition from weeds (Bond & Grundy 2001). Tillage is often assumed to be an effective means of mechanical control for slugs (AHDB 2015), although recent evidence casts doubt over its effectiveness to control soil-associated pests, while this practice can worsen foliar pest abundance and suppress soil-associated predators (Rowen et al. 2020). Therefore, appropriate crop selection, for example rotations based around oats, may be a more effective means of reducing slug damage (Douglas & Tooker 2012), while avoiding adverse effects on beneficial biodiversity from high-disturbance tillage. Further recommendations with regard to the tree row understorey are discussed below.

Which arable crops are best suited to agroforestry systems?

The yield data reported in Chapter 6 implies that relative yields, i.e. yields in agroforestry relative to arable systems, are higher for oats than for barley or wheat. However, there is low confidence in this conclusion because crop type was confounded with site, therefore, this requires further validation. Nevertheless, this conclusion could be expected given the relative resistance of oats to weed pressure and slug damage, as discussed in Chapter 6. Data were not available for other crop types, including break crops such as oilseed rape or field bean, but these crops could be particularly affected by slug damage (AHDB 2015). We would also predict that mass-flowering crops with long flower structure, such as field beans, would receive better relative pollination (i.e. pollination in agroforestry relative to arable) than those with open flower structures, such as oilseed rape, based on the community-level pollinator effects in Chapter 4.

How to manage the tree row understorey?

Chapter 5 provides evidence from one case-study site to support the common practice of establishing flower strips with low intensity management in agroforestry systems (Newman et al. 2018), as was applied to all three sites in Chapters 3 and 4. Unmown flowering understoreys supported higher natural enemy diversity, higher early-season counts of natural enemies in fruit trees, and fewer aphids and aphid-damaged apples than mown understoreys. However, to maintain flower cover and richness in the long-term and suppress competitive grasses, twice-yearly mowing of wildflower strips would be advisable, while maintaining an unmown strip as an insect refuge (Piqueray et al. 2019). A practical location for this unmown strip would be the central part of the tree rows, between the trunks.

To minimise weed pressure, management should aim to promote a continuous sward in the understorey, to minimise opportunities for weeds to colonise via seed-spread (Moonen & Marshall 2001). Understorey management may need to be adjusted to target any problematic species, for example, by increasing the frequency of cutting to deplete root carbohydrate stores of perennial weeds (Hatcher & Melander 2003).

Alternative and unstudied approaches for ecological management of the tree row understorey could be to use a legume-based mix, which is frequently practiced for cover cropping in orchards, and has nitrogen fixation benefits (Crézé & Horwath 2021). Another option would be to promote ‘beetle-bank’ vegetation of coarse grasses which require little management and have good competitive advantage over colonising weeds (MacLeod et al. 2004), but are likely to compete more severely with apple trees for water and nutrients.

How to minimise economic risk in agroforestry systems?

Productivity and price of the tree crop (in this case apples) were identified as the major factors determining farm income from agroforestry systems in Chapter 6. Similarly, studies of timber- and nut-arable agroforestry systems concluded that their profitability is heavily dependent on receiving a high value for the tree product (Graves et al. 2007; Sereke et al. 2015; Toor et al. 2012). This demonstrates the need for agroforestry farmers to develop skills in tree management, such as pruning, especially given that most adopters of these agroforestry systems are arable and/or livestock farmers with limited prior experience in tree crop production. In addition, it is important to identify high-value markets such as premium products or local specialities (as practiced by the study site in Chapter 5).

How wide should crop alleys be?

Although the width of crop alleys was not explicitly tested, very few spatial effects were observed across alleys in Chapters 3 and 4, including minor but significant effects on taxonomic richness of plants and invertebrates, and hoverfly abundance. This suggests substantial spill-over of beneficial fauna from the tree rows into the crop alleys, but also implies that biodiversity would gradually decline with increasing alley width. This is supported by distance-decay patterns from agri-environment scheme features into arable fields (Albrecht et al. 2020; Boetzl et al. 2019; Woodcock et al. 2016), although these can depend on crop type and landscape context (Boetzl et al. 2020). Furthermore, different spill-over patterns of predatory invertebrates have been observed in organic versus conventional systems, suggesting that tree rows in conventional systems have a sink and retention effect rather than providing a source and spill-over (Boinot et al. 2020). Therefore, this issue appears to be complex and could be heavily dependent on confounding variables such as farm management and landscape context.

7.5 Concluding remarks: how to promote the uptake of agroforestry and other diversified farming systems?

Diversified farming systems and other forms of ecological intensification of agriculture are needed to halt biodiversity losses, mitigate climate change, and sustain productivity (FAO 2013; Kremen & Miles 2012; Lichtenberg et al. 2017). Despite recognition amongst governments and scientists of this pressing need, the adoption of diversified farming systems in temperate regions has been limited, indicating a substantial gap between science and practice (Chaplin-Kramer et al. 2019; Kleijn et al. 2019). This is particularly pertinent to agroforestry systems, the extent of which is substantially lower than the potential targeted extent (Reisner et al. 2007). Reporting of farmer-relevant outcomes such as profit, productivity and risk by scientists has been identified as a key barrier to the uptake of diversified farming systems (Chaplin-Kramer et al. 2019; Kleijn et al. 2019), while agroforestry-specific barriers include lack of technical knowledge, capital investment requirements, uncertainty regarding support payments, availability of suitable case studies and demonstration sites, increased labour, and administrative complexity (García de Jalón et al. 2018; Raskin 2020; Rois-Díaz et al. 2018).

Possible solutions to these barriers are summarised in Figure 7.4, which emphasises the potential role of scientific research in driving adoption through effective communication to practitioners and policy-makers, which in turn leads to improved recognition and support of agroforestry systems in national agricultural policies, peer-to-peer learning and case studies, effective marketing of agroforestry products, and improved links between science and practice through stakeholder engagement (Kröbel et al. 2021; Sollen-Norrlin et al. 2020). This thesis ultimately aims to contribute to this solution by providing an evidential basis to inform future research directions and to advise practitioners and policy-makers, which will be communicated through ongoing dissemination.

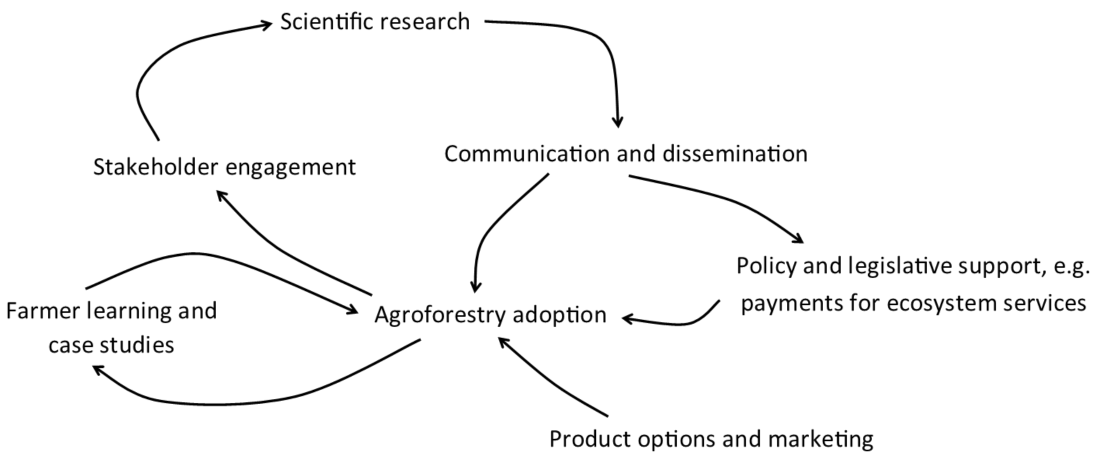
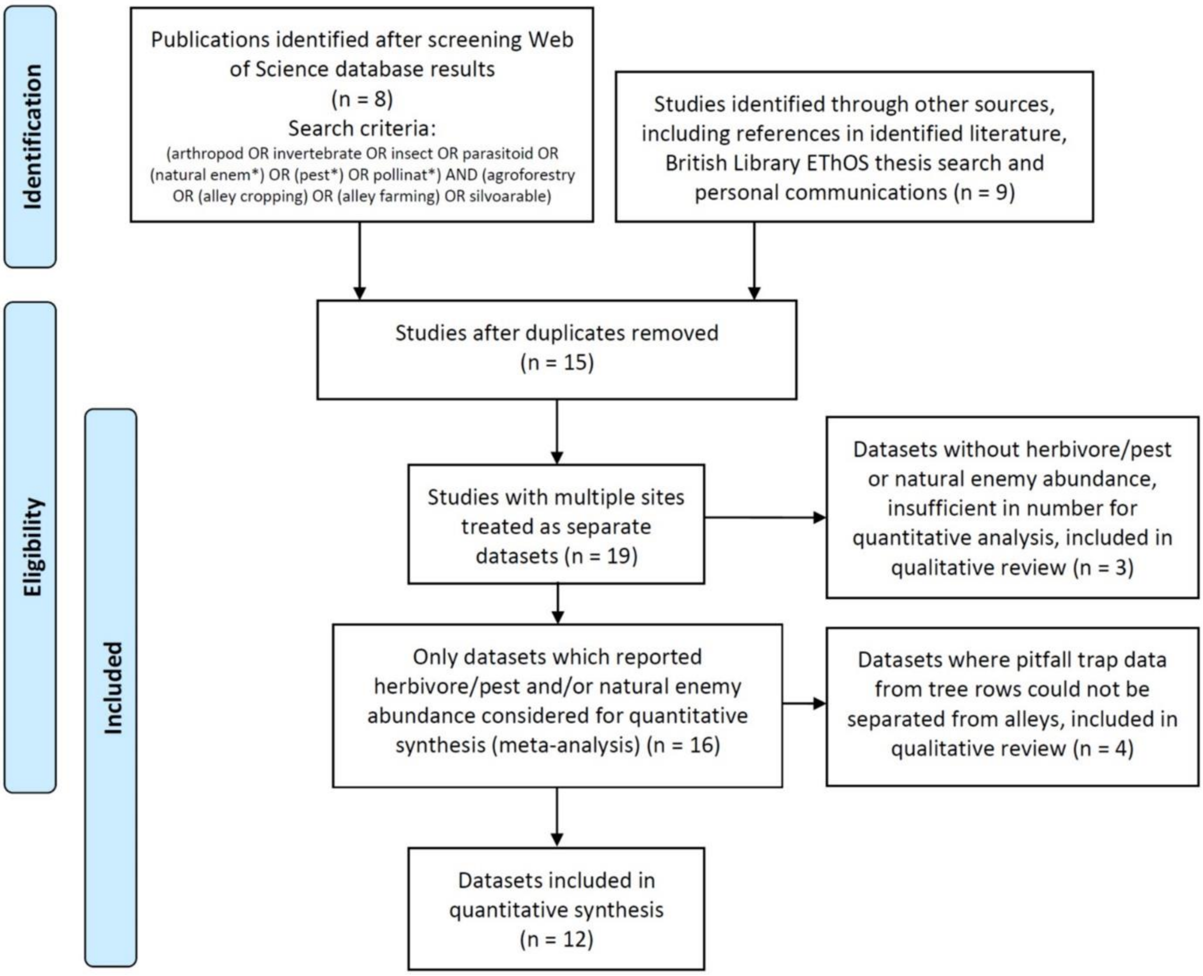


Figure 7.4. Conceptual framework as to how scientific research can drive the adoption of agroforestry systems through stakeholder engagement and communication.

8. Appendices

8.1 Appendix 1: literature selection (Chapter 2)

This appendix comprises a flow diagram for literature selection based on PRISMA (Moher et al. 2009):



8.2 Appendix 2: Meta-analysis effect sizes (Chapter 2)

This appendix comprises a table of effect sizes of natural enemy and pest/herbivore abundances or activity densities (used to inform Fig. 2.3):

Reference	**Natural enemies**		**Pests / herbivores**		**Tree row data included?**	**Standard deviations imputed?**
	Taxa	**Effect size**	**Taxa**	**Effect size**		
Peng et al. (1993)	All airborne predators and parasitoids	1.43	All airborne pests	1.13	Excluded	Imputed
Phillips et al. (1994)	Carabidae species (3), *Tachyporus hypnorum*, aphidophagous hoverflies	1.25	-	-	Excluded	Extracted from study
Peng and Sutton (1996)	Carabidae species (10), Coccinellidae, Linyphiidae, Lycosidae	1.14	*Sitona lineatus*	0.85	Excluded	Imputed
Naeem et al. (1997); Naeem et al. (1994)	-	-	*Sitobion avenae*	0.53	Excluded	Extracted from study
Griffiths et al. (1998)	-	-	Slugs	1.53	Excluded (refuge trap data used)	Extracted from study
Howell (2001)	All airborne predators and parasitoids	1.34	All airborne herbivores.	0.58	Included	Extracted from study
Stamps et al. (2002)	All predators and parasitoid Hymenoptera (sweep netting)	1.67	All herbivores (sweep netting)	0.69	Included	Extracted from study
Akbulut et al. (2003)	Carabidae, Chalcidoidea, Araneae	1.45	-	-	Included (but pitfall traps not sampled in tree rows)	Extracted from study
Burgess et al. (2003): Leeds site only	Araneae, Carabidae	0.71	Slugs	1.12	Excluded	Imputed
Muhammad et al. (2005)	-	-	*Sitobion avenae*	0.46	Excluded	Extracted from study
Smits et al. (2012)	Syrphidae, Coccinellidae, Neuroptera (all life-stages)	1.03	Aphids	1.01	Excluded	Extracted from study
Sharman (2015)	Carabidae	1.54	-	-	Excluded (by excluding all fields with possible tree row data and corresponding controls, i.e. S1, S2, A1, A2)	Imputed

Studies not included in meta-analysis because pitfall trap data from tree rows could not be separated:						
Burgess et al. (2003): Cirencester and Silsoe sites	Araneae, Carabidae, Staphylinidae	0.39	Slugs	2.73	Included	N/A
		0.64		0.73		
Rekany (2015): 2 silvoarable sites	Araneae, Carabidae	0.59	-	-	Included (not known whether tree row data was included in experimental design for comparison with arable)	N/A
		1.58				

8.3 Appendix 3: Field sites

This appendix contains descriptions and photographs of field sites used for data collection. The sites used for sampling from the arable components contained an agroforestry field and arable field under the same management. The agroforestry fields were configured with 3-4 m wide tree rows, separated by 24 m wide arable crop alleys. Sites 1-3 (corresponding to table rows) were used for Chapters 3 and 4, site 1 was used for Chapter 5, and all five sites were used in Chapter 6 (with site 3 comprising the case study site).

Table A3.1. Descriptions of field sites. AF = agroforestry, Con = arable control.

Location	**Latitude / longitude**	**Management**	**Date trees planted**	**Soil texture**	**Tree species**	**Tree row understorey**	**Crop harvest during sampling**	**General crop rotation**	**Yield samples taken**	**Approx. field sizes (ha)**
Nottinghamshire, UK	52°59'19''N 0°54'38''W	Conventional, minimum-tillage	Early 2014	Clayey	21 apple vars + 3 native tree sp.	Wildflower mix. 50% (outer edge) cut mid-summer.	Winter wheat (2019), spring barley (2020)	Oilseed rape, winter or spring wheat or barley (2 yrs)	Arable, apple (Braeburn and Bramley)	5.6 (AF) 6.1 (Con)
Cambridgeshire, UK	52°24'47''N 0°13'14''E	Organic	Early 2015	Clayey	5 apple vars + 28 tree sp.	Clover mix. Flexible management, usually twice per year.	Winter wheat (2018), winter oats (2019)	Winter wheat, winter oats, clover ley (2 yrs)	Arable	3.8 (AF) 3.0 (Con)
Cambridgeshire, UK	52°31'54''N 0°11'31''E	Organic	Late 2009	Peaty	13 apple vars.	Wildflower mix. 50% (outer edge) cut mid-summer. In Countryside Stewardship.	Winter oats (2018, 2019)	Winter oats, irregular fallow break	Arable, apple (Bramley)	12.0 (AF) 7.6 (Con)

Oxfordshire, UK	51°29'47"N 1°3'55"W	Organic	Early 2015	Loamy	18 apple vars. + 7 timber sp.	Wildflower mix, low intensity management	N/A	Vegetables	Apple (Bramley)	2.4 (AF)
Norfolk, UK	52°30'20"N 1°34'53"E	Conventional	Early 2017	Loamy, some clayey	20 apple vars., other fruit/nut species	Grass / clover mix	N/A	Mixed rotation of vegetables and pasture	Apple (Braeburn and Bramley)	5.3 (AF)

Figure A3.1: Photographs of (from left to right, top row then lower row): Site 1, taken May 2019; Site 2, taken May 2018; Site 3, taken November 2019; Site 4, taken September 2020; Site 5, taken August 2020. Site numbers correspond to the rows in Table A3.1.

8.4 Appendix 4: Experimental design and sampling methodology

This appendix shows the locations and arrangement of sampling points at each site (Fig. A4.1), describes the sampling methods used and their frequency and duration (Table A4.1) with further detail on sampling frequency at Table A4.2, and the number of samples not included in the analysis due to trap damage (Table A4.3).

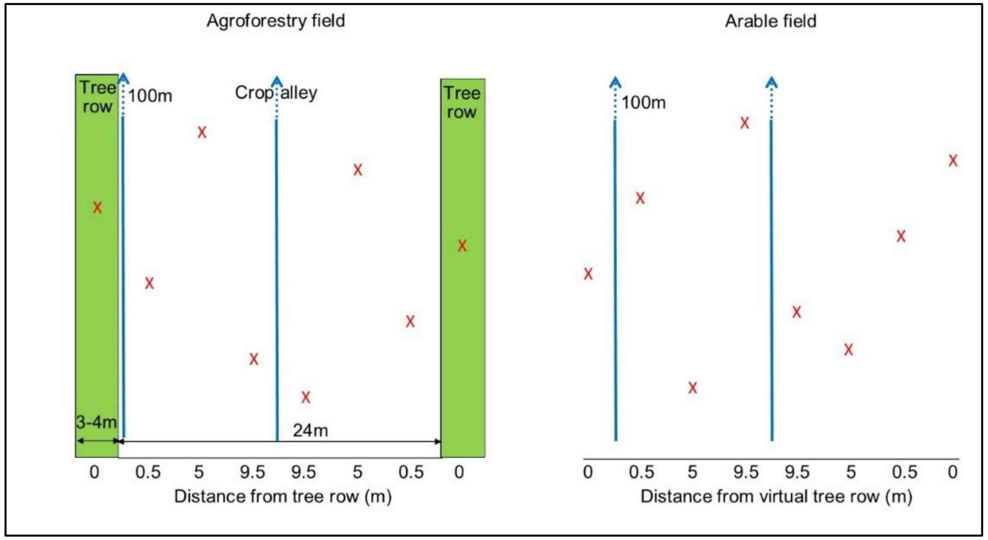


Figure A4.1. Schematic (not to scale) of sampling points (red crosses) and transects (blue lines) within the agroforestry and arable fields. Positioning parallel to the tree row was randomly staggered by multiples of 5 m to account for the possibility of fauna moving out into the alleys from the tree rows. The figure just shows one alley. In practice two adjacent agroforestry alleys were sampled at each of the three sites, and this procedure was repeated in the arable field within ‘virtual alleys’. The positioning of samples from different methods were slightly offset by a consistent distance parallel to the tree row to avoid interference.

Table A4.1. Summary of plant and invertebrate sampling methods, frequency and duration.

Objective	Sampling method	Protocol for each sampling point	Duration of each sample	Number of sampling periods per site (2018/9)	Summary of main limitations
Epigeal arthropod community, pest abundances	Pitfall trapping	Plastic cup, 70 mm diameter x 100 mm depth. Wire mesh (30 mm) fitted over top to prevent mammal captures. Trapping fluid: ethylene glycol (2018) or propylene glycol (2019), diluted to 1/6 and 1/4 concentration respectively, with small amount of scentless detergent. Total 60 ml, or 120 ml in very hot weather.	4 to 20 days	8 to 10 per site	Capture rates are determined by both the abundance and ground-activity of a species, therefore, this technique is sensitive to biases associated with habitat structure and searching activity (Lang 2000; Woodcock 2005). To mitigate this, pitfall traps from tree rows were not analysed, as the vegetation structure was different to arable.
Airborne arthropod community, pest abundances	Pan (water) trapping	Plastic bowls, 150 mm diameter x 40 mm depth. Three colours at each sampling point: UV reflective yellow, blue and white. Trapping fluid: 200 ml of water with small amount of scentless detergent. Placed on ground, or elevated on stake (1.2 or 1.5 m) when crop height > 40 cm. Trapping was only undertaken during suitable weather conditions, i.e. maximum temperature of at least 13 ˚C, maximum wind speed less than 25 mph, and no rain. As pollen beetle (*Brassicogethes* spp.) counts were very high in some cases, abundance was estimated by weighing and comparing to the mean average weight of 100 beetles based on three haphazardly-selected samples from different locations.	5 to 9 hours	9 per site	Capture rates depend on the attraction of each species to pan colour, therefore the method is prone to biases in proportional abundance of taxa (Vrdoljak & Samways 2012). In addition, abundant floral resources may reduce capture rates of flower-visitors by reducing their searching activity (Baum & Wallen 2011; O'Connor et al. 2019).
Aphid abundance	Crop assessment	Count of aphids on crop, 20 tillers per sample point. Attempted at all three sites, but sufficient quantity of aphids only at one site.	-	Once	-

Plant communities	Quadrat	1 x 1 m square quadrat, all vascular plant species recorded (where possible) with percentage cover and number of flowers. Only sampled in arable areas (i.e. not tree rows).	-	Two per site (i.e. once per year)	Cover data subject to recorder bias. To mitigate this, all quadrats were recorded by the same person.

Table A4.2. Timing of sampling methods at each site. Each number represents the date (or date range) within that month the sampling was carried out. Site numbers refer to rows in Appendix 3 (Table A3.1).

Sampling technique	**Site**	**2018**						**2019**						
		May	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**
Pitfall trapping	1	9-22	13-22	6-16	16-20	28-2Oct	-	10-18	15-22	18-27	-	-	-	24-31
	2	10-19	14-21	18-1Aug	21-25	26-2Oct	19-24	23-2May	13-21	19-28	-	-	-	17-24
	3	8-18	15-22	19-8Aug	-	27-2Oct	-	9-17	14-21	20-28	-	-	-	31-10Nov
Pan trapping	1	22	13	1Aug	16	28	-	18	15	-	3	-	13	-
	2	19	21	18	21	26	19	23	13	-	1Aug	-	-	-
	3	18	15	19	25	27	-	17	14	-	2	-	14	-
Plant quadrats	1	-	13	-	-	-	-	-	22	-	-	-	-	-
	2	-	14	-	-	-	-	-	21	-	-	-	-	-
	3	-	22	-	-	-	-	-	21	-	-	-	-	-
Aphid crop assessment	1	-	-	-	-	-	-	-	-	-	3	-	-	-

Table A4.3. Number of samples damaged (out of 28 or 32 at each site/method/month for pitfall and pan traps respectively) and thus not included in analysis. This includes flooded or damaged pitfall traps and dislodged pan traps from bird disturbance. Site numbers refer to rows in Appendix 3 (Table A3.1).

Sampling technique	**Site**	**2018**						**2019**						
		May	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**
Pitfall trapping	1	0	2	1	0	7	-	0	0	0	-	-	-	9
	2	0	0	2	0	0	0	2	1	0	-	-	-	0
	3	7	1	2	-	15	-	0	1	0	-	-	-	0
Pan trapping	1	8	1	0	0	0	-	0	0	-	0	-	0	-
	2	1	2	1	0	0	0	0	0	-	0	-	-	-
	3	2	3	1	0	0	-	0	1	-	0	-	0	-

8.5 Appendix 5: Taxonomic resolution (Chapters 3 and 5)

This appendix sets out taxonomic resolution of specimens captured in pitfall, sticky, and pan traps, with identification literature. This covers adult invertebrate specimens. Larvae were identified to Order level. Plants were recorded to species level where possible. Years 2018 and 2019 refer to Chapter 3, 2020 to Chapter 5.

Taxon	**Taxonomic resolution of records**	**Literature used for identification**
Insects		
Carabid beetles (Coleoptera: Carabidae)	Species or genus (for *Amara* and *Bembidion*)	Luff, L.M., 2007. The Carabidae (ground beetles) of Britain and Ireland (2nd ed.). Shrewsbury: Field Studies Council.
Ladybirds (Coleoptera: Coccinellidae)	Species, except Coccidulinae to sub-family	UK ladybird survey (https://www.coleoptera.org.uk/coccinellidae/home)
Sap beetles (Coleoptera: Nitidulidae)	*Glischrochilus* and *Meligethes* to genus, otherwise to family	Unwin, D.M., 1988. A key to the families of British beetles. Shrewsbury: Field Studies Council. https://www.coleoptera.org.uk/
Carrion beetles (Coleoptera: Silphidae)	*Nicrophorus* and *Silpha* to genus, otherwise to family	Unwin, D.M., 1988. A key to the families of British beetles. Shrewsbury: Field Studies Council. https://www.coleoptera.org.uk/
Rove beetles (Coleoptera: Staphylinidae)	Family (in 2018) or sub-family (in 2019 and 2020), except *Ocypus olens* to species in all years, and Mycetoporini/Tachyporini to tribe in 2019	Unwin, D.M., 1988. A key to the families of British beetles. Shrewsbury: Field Studies Council. Lott, D.A., 2009. The Staphylinidae (rove beetles) of Britain and Ireland Part 5: Scaphidiinae, Piestinae, Oxytelinae. Shrewsbury: Field Studies Council.
All other beetles (Coleoptera)	Family, except *Oedemera nobilis* to species and *Malachius* and *Psylliodes* to genus	Unwin, D.M., 1988. A key to the families of British beetles. Shrewsbury: Field Studies Council. https://www.coleoptera.org.uk/

Earwigs (Dermaptera)	Order	Tilling, S.M., 2014. A key to the major groups of British terrestrial invertebrates (2nd ed.). Shrewsbury: Field Studies Council.
Flies (Diptera), except hoverflies (Syrphidae)	Family, Calliphoridae/Muscidae grouped	Unwin, D.M., 1981. A key to the families of British Diptera. Shrewsbury: Field Studies Council.
Hoverflies (Diptera: Syrphidae)	Species or genus (genus in 2020)	Stubbs, A.E. & Falk, S.J., 2002. British hoverflies (2nd ed.). Reading: British Entomological and Natural History Society. Ball, S. & Morris, R., 2015. Britain's hoverflies (2nd ed.). Oxfordshire: Princeton University Press.
Heteroptera (Hemiptera: Heteroptera)	Suborder (Heteroptera), family or sub-family in 2020	Unwin, D., 2001. A key to the families of British bugs (Insecta, Hemiptera). Shrewsbury: Field Studies Council.
Homoptera (Hemiptera: Homoptera)	Superfamily or family, *Sitobion avenae* to species in 2019	
Bees (Hymenoptera: Anthophila)	Family (in 2018) or genus (in 2019 and 2020), except *Bombus* identified to genus (all years), *Apis mellifera* to species (all years)	Falk, S. & Lewington, R., 2017. Field guide to the bees of Great Britain and Ireland. London: Bloomsbury.
Ants (Hymenoptera: Formicidae)	Family (Formicidae)	-
Parasitoid wasps (Hymenoptera: Parasitica)	'Parasitica' (paraphyletic) in 2018, in 2019 and 2020 Braconidae, Ichneumonidae and Chrysidoidea separated	Yeo, P.F. & Corbet, S.A., 1995. Solitary wasps (2nd ed.). Exeter: Pelagic Publishing. Goulet, H. & Huber, J.T. (Eds.) 1993. Hymenoptera of the world: an identification guide to families. Ontario: Agriculture Canada.
Sawflies (Hymenoptera: Symphyta)	Suborder (Symphyta), except *Cephus* to genus	Yeo, P.F. & Corbet, S.A., 1995. Solitary wasps (2nd ed.). Exeter: Pelagic Publishing.
Social wasps (Hymenoptera: Vespidae)	Family (Vespidae)	
Other Hymenoptera	Family or genus	
Butterfly adults (Lepidoptera, part)	Species (if possible depending on preservation)	https://butterfly-conservation.org/
Other Lepidoptera	Order (Lepidoptera)	Tilling, S.M., 2014. A key to the major groups of British terrestrial invertebrates (2nd ed.). Shrewsbury: Field Studies Council.
Lacewings (Neuroptera)	Order (Neuroptera)	
Dragonflies (Odonata: Anisoptera)	Infraorder (Anisoptera)	

Damselflies (Odonata: Zygoptera)	Suborder (Zygoptera)	
Grasshoppers and crickets (Orthoptera)	Superfamily	
Booklice (Psocoptera)	Order (Psocoptera)	
Fleas (Siphonaptera)	Order (Siphonaptera)	
Thrips (Thysanoptera)	Order (Thysanoptera)	
Other arthropods		
Mites (Acari)	Subclass (Acari), except *Eutrombidium* to genus in 2019 and 2020	Tilling, S.M., 2014. A key to the major groups of British terrestrial invertebrates (2nd ed.). Shrewsbury: Field Studies Council.
Spiders (Araneae)	Order (in 2018), in 2019: family, except Clubionidae, Pisauridae and Tetragnathidae, to genus. Lower-level taxa imputed for 2018 pRDA analyses based on proportions at each site/treatment. In 2020, family or genus.	Roberts, M.J., 1996. Collins field guide: Spiders of Britain and northern Europe. London: HarperCollins Publishers.
Centipedes (Chilopoda)	Order	Tilling, S.M., 2014. A key to the major groups of British terrestrial invertebrates (2nd ed.). Shrewsbury: Field Studies Council.
Springtails (Collembola)	Sub-class (Collembola), only recorded in 2019 and 2020	
Millipedes (Diplopoda)	Class (Diplopoda)	
Slugs (Gastropoda, part)	Genus or species, except some juveniles recorded as ‘slug’	Rowson, B., Turner, J., Anderson, R. & Symondson, B., 2014. Slugs of Britain and Ireland. Telford: FSC Publications.
Snails (Gastropoda, part)	‘Snail’ (polyphyletic)	-
Leeches (Hirudinea)	Subclass (Hirudinea)	Tilling, S.M., 2014. A key to the major groups of British terrestrial invertebrates (2nd ed.). Shrewsbury: Field Studies Council.
Woodlice (Isopoda)	Order (Isopoda)	
Worms (Oligochaeta)	Subclass (Oligochaeta)	
Harvestmen (Opiliones)	Order (Opiliones)	
Pseudoscorpions (Pseudoscorpiones)	Order (Pseudoscorpiones)	

8.6 Appendix 6: model outputs (Chapter 3)

This appendix sets out model selection and outputs for linear models, mixed models and generalized linear models, in Chapter 3. Fixed effect estimates above 0 represent positive association with agroforestry relative to arable. A '-' under random effects denotes where that random effect was not applied to the model because there was only one level.

Response	**Family and link (if GLM)**	**Fixed effect (farming system)**				**Month/Year (random effect)**		**Site (random effect)**		**Residual**		**R-squared (marginal)**	**R-squared (conditional)**	**Data subsetting**
		Estimate	**SE**	**T or z value**	**P-value**	**Variance**	**SD**	**Variance**	**SD**	**Variance**	**SD**			
Richness (Fig. 3.3)														
Plants	-	0.971	0.177	5.478	<0.001	0.895	0.946	1.223	1.106	1.198	1.095	0.065	0.657	-
All invertebrates	-	1.694	0.451	3.756	<0.001	21.56	4.644	3.900	1.975	32.58	5.707	0.012	0.441	-
Herbivores	-	0.604	0.163	3.701	<0.001	2.494	1.579	0.191	0.437	4.267	2.066	0.013	0.390	-
Natural enemies	-	0.057	0.300	0.189	0.85	5.300	2.302	0.607	0.779	14.38	3.792	<0.001	0.288	-
Shannon diversity (Fig. 3.3)														
Plants	-	0.270	0.056	4.852	<0.001	0.170	0.413	0.045	0.213	0.118	0.343	0.051	0.659	-
All invertebrates	-	0.146	0.043	3.401	<0.001	0.274	0.524	0.052	0.227	0.294	0.542	0.008	0.526	-
Herbivores	-	0.123	0.028	4.439	<0.001	0.073	0.270	0.029	0.171	0.123	0.350	0.016	0.458	-
Natural enemies	-	0.070	0.037	1.898	0.058	0.059	0.244	0.011	0.104	0.219	0.468	0.004	0.243	-
Natural enemies (Fig. 3.4)														
Functional diversity	-	0.025	0.008	3.249	0.001	0.007	0.082	<0.001	0.017	0.008	0.087	0.010	0.481	-
Phylogenetic diversity	-	0.004	0.009	0.409	0.683	0.002	0.040	<0.001	0.021	0.011	0.104	<0.001	0.161	-

Decoupled phylogenetic diversity	-	0.008	0.005	1.563	0.119	<0.001	0.025	<0.001	0.007	0.003	0.058	0.004	0.166	-
Pests / weeds (Fig. 3.5)														
Pollen beetles	Negative binomial, log	-0.837	0.152	-5.518	<0.001	-	-	-	-	1.046	1.023	0.141	0.141	Pan traps, site 1, June 2018
Root flies	Negative binomial, log	-0.473	0.062	-7.627	<0.001	1.680	1.293	0.574	0.758	1.028	1.014	0.018	0.761	Pan traps
Wheat stem sawfly	Negative binomial, log	-0.455	0.205	-2.225	0.026	-	-	-	-	1.170	1.082	0.038	0.038	Pan traps, site 2, June 2018
Aphids	Poisson, log	0.051	0.124	0.409	0.682	-	-	-	-	6.215	2.493	0.006	0.006	Crop assessment, site 1
Frit flies	Negative binomial, log	0.051	0.081	0.637	0.524	0.965	0.982	0.227	0.476	0.989	0.995	<0.001	0.505	Pan traps
Click beetles / wireworms	Negative binomial, log	0.176	0.251	0.700	0.484	0.078	0.280	0.604	0.777	0.435	0.659	0.001	0.116	Pitfall traps, June & July 2018, April, May & June 2019
Non-crop plant cover	Negative binomial, log	0.286	0.083	3.462	<0.001	0.039	0.197	0.034	0.186	0.995	0.997	0.074	0.341	Quadrats, sites 2 and 3
Slugs	Negative binomial, log	0.324	0.121	2.686	0.007	0.415	0.644	0.030	0.174	0.994	0.997	0.017	0.318	Pitfall traps, sites 1 and 2, May, June & October 2018 and 2019

8.7 Appendix 7: taxon abbreviations

This appendix sets out abbreviations for taxa shown in Figure 3.2. This is not a list of all species recorded, only the most abundant species are listed as stated at the Figure 3.2 caption.

Abbreviation	**Full name**	**Common name**
Plants		
Alo.myos	*Alopecurus myosuroides*	Black-grass
Cir.arve	*Cirsium arvense*	Creeping Thistle
Con.arve	*Convolvulus arvensis*	Field Bindweed
Gal.apar	*Galium aparine*	Cleavers
Pap.rhoe	*Papaver rhoeas*	Common Poppy
Per.lapa	*Persicaria lapathifolia*	Pale Persicaria
Poa.triv	*Poa trivialis*	Rough Meadow-grass
Ste.medi	*Stellaria media*	Chickweed
Ver.pers	*Veronica persica*	Common Field-speedwell
Vio.arve	*Viola arvensis*	Field Pansy
Herbivores		
Anthomy.	Anthomyiidae	Root flies
Aphidida.	Aphididae	Aphids
Bibionid.	Bibionidae	March flies
Brassico.	*Brassicogethes*	Pollen beetles
Cecidomy.	Cecidomyiidae	Gall midges
Chloropi.	Chloropidae	Frit flies
Cicadell.	Cicadellidae	Leafhoppers
Diplopod.	Diplopoda	Millipedes
Sciarida.	Sciaridae	Fungus gnats
Thysanop.	Thysanoptera	Thrips
Natural enemies		
A. dors.	*Anchomenus dorsalis*	A ground beetle
Bembidi.	*Bembidion*	A ground beetle
Braconi.	Braconidae	Braconid parasitoids

Dolicho.	Dolichopodidae	Long-legged flies
Empidid.	Empididae	Dance flies
Episyrp.	*Episyrphus*	A hoverfly
Eupeode.	*Eupeodes*	A hoverfly
H. rufi.	*Harpalus rufipes*	A ground beetle
Linyphi.	Linyphiidae	Money spiders
Lycosid.	Lycosidae	Ground or wolf spiders
N. brev.	*Nebria brevicollis*	A ground beetle
Opilion.	Opiliones	Harvestmen
Parasit.	Parasitica	Parasitoid wasps
P. mela.	*Pterostichus melanarius*	A ground beetle
Sphaero.	*Sphaerophoria*	A hoverfly
Staphyl.	Staphylininae	A rove beetle sub-family
Tachypo.	Tachyporini	A rove beetle sub-family

8.8 Appendix 8: seasonality analysis (Chapter 3)

This appendix sets out a partial redundancy analyses with seasonality (month/year, as a factor) as the single explanatory variable. Separate analyses were undertaken for arable and agroforestry systems. Explanatory variables are shown in red, with response variables (traits) shown in black. Site was a ‘partialled out’ covariate.

Figure A8.1. Seasonality pRDAs, for herbivorous invertebrates (top row) and natural enemy invertebrates (bottom row), undertaken separately for agroforestry systems (left) and arable systems (right).

8.9 Appendix 9: spatial analysis (Chapter 3)

This appendix sets out spatial analyses of diversity metrics and pest abundances across agroforestry alleys.

Table A9.1. Summary statistics for spatial pRDAs based on 999 permutations. 'Distance from tree row' was the single explanatory variable and taxa or traits for each trophic level were response variables. The analysis was not run for plants because only two sites were available.

Trophic level	Response	F value	p-value
Natural enemies	Taxa	1.390	0.129
	Traits	1.186	0.287
Herbivores	Taxa	0.983	0.408
	Traits	1.138	0.298

Table A9.2. Outputs of mixed models for diversity metrics for each trophic level, with distance from tree row as the single explanatory variable. Fixed effect estimates represent the change in the diversity metric for each metre away from the tree row. Site and month/year were included as random intercept effects.

Trophic level	Response variable	Fixed effect estimate	Fixed effect standard error	t value	p-value
Plants	Richness	-0.103	0.035	-2.919	0.005
	Shannon diversity	-0.021	0.011	-1.893	0.063
Herbivores	Richness	-0.110	0.034	-3.242	0.001
	Shannon diversity	-0.021	0.006	-3.622	<0.001
Natural enemies	Richness	-0.069	0.059	-1.185	0.237
	Shannon diversity	-0.008	0.007	-1.152	0.250
	Phylogenetic diversity	0.001	0.002	0.603	0.547
	Functional diversity	<0.001	0.002	-0.093	0.926
All invertebrates	Richness	-0.204	0.087	-2.339	0.020
	Shannon diversity	-0.013	0.008	-1.491	0.137

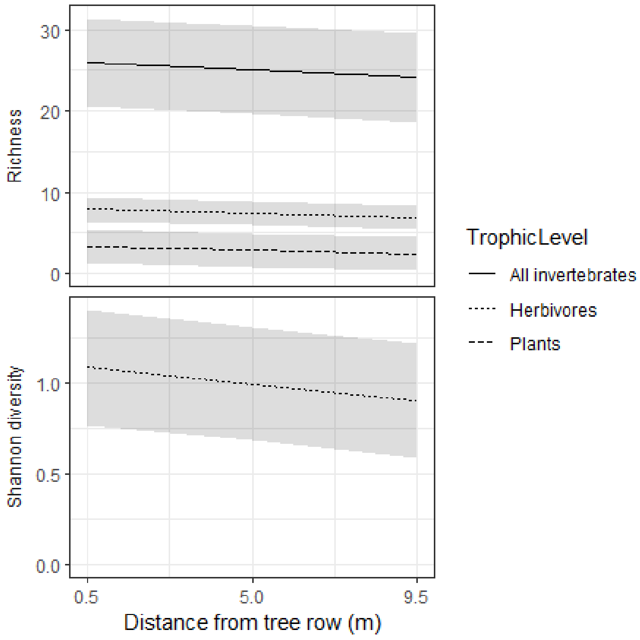


Figure A9.1. Diversity and richness patterns across agroforestry alleys, based on predictions from the models set out in the Table 9.2. Grey lines indicate 95% confidence intervals. Only the models with a p-value less than 0.05 are shown.

Table A9.3. Outputs of generalized linear models for pest abundances in agroforestry systems, where distance from tree row was the single explanatory variable. Fixed effect estimates represent the log change in pest abundance for each metre away from the tree row. The data was subset as set out in Appendix 6. NB = negative binomial, GLM = generalized linear model, GLMM = generalized linear mixed model.

Taxon	**Fixed effect estimate**	**Fixed effect standard error**	**z value**	**p-value**	**Model**
Pollen beetles	0.048	0.037	1.324	0.185	NB GLM
Root flies	0.001	0.011	0.073	0.942	NB GLMM
Wheat stem sawfly	0.083	0.038	2.199	0.028	NB GLM
Aphids	0.042	0.074	0.576	0.565	NB GLM
Frit flies	0.027	0.014	1.865	0.062	NB GLMM
Click beetles / wireworms	0.061	0.032	1.902	0.057	Poisson GLMM
Non-crop plant cover	-0.019	0.014	-1.397	0.162	NB GLMM
Slugs	0.008	0.024	0.318	0.750	NB GLMM

8.10 Appendix 10: seasonal patterns in richness and diversity (Chapter 3)

This appendix sets out plots of seasonal patterns of richness and diversity, broken down by month/year. Separate plots are presented for all invertebrates, herbivorous invertebrates and invertebrate natural enemies. Each plot was also tested for significance within a mixed model, with farming system and month/year as fixed interaction effects and site as a random effect. May 2018 was the reference level for month/year and arable was the reference for farming system. Significant interaction effects are shown on the right side of the graph (p-values represented by: ***<0.001, **<0.01, *<0.05, †<0.10), along with '+' or '-' to represent whether the significant interaction with farming system was positive or negative.

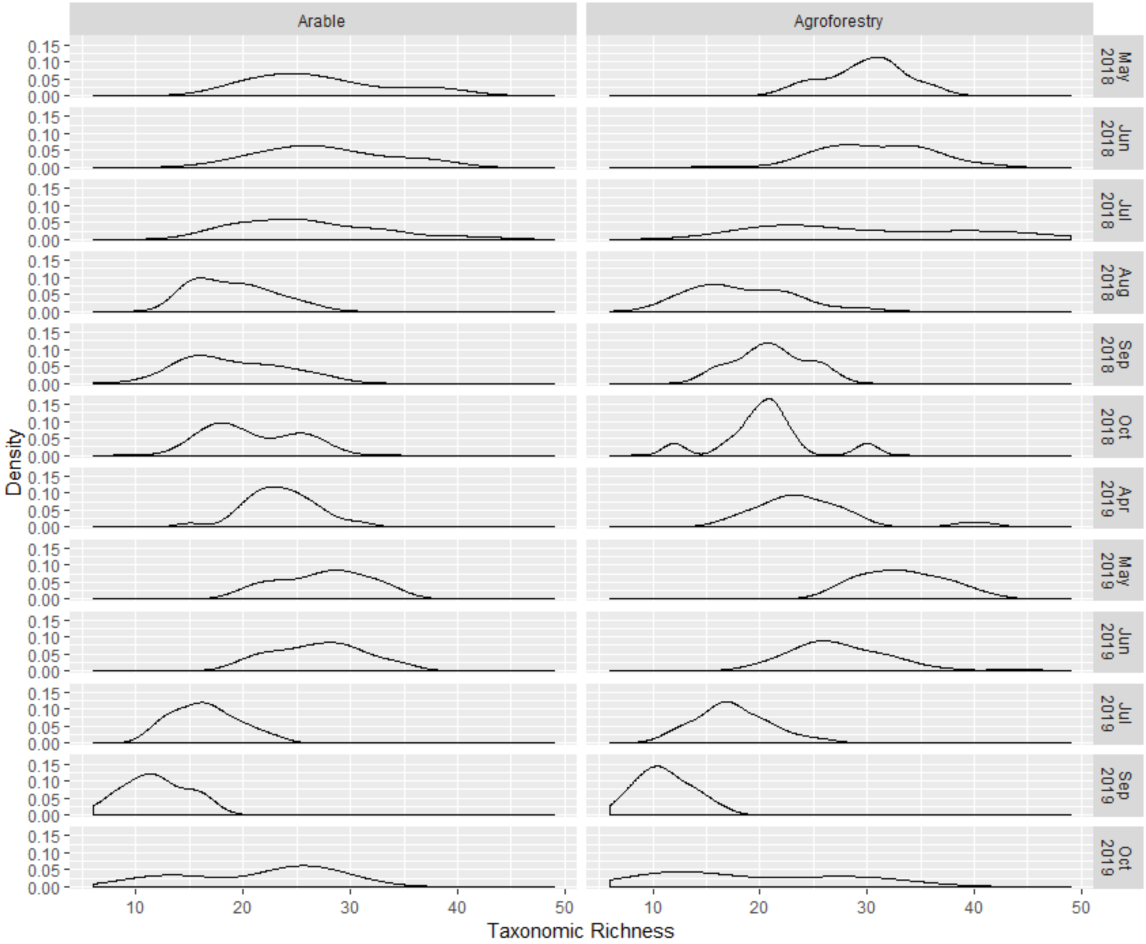


Figure A10.1. Taxonomic richness for all invertebrates.

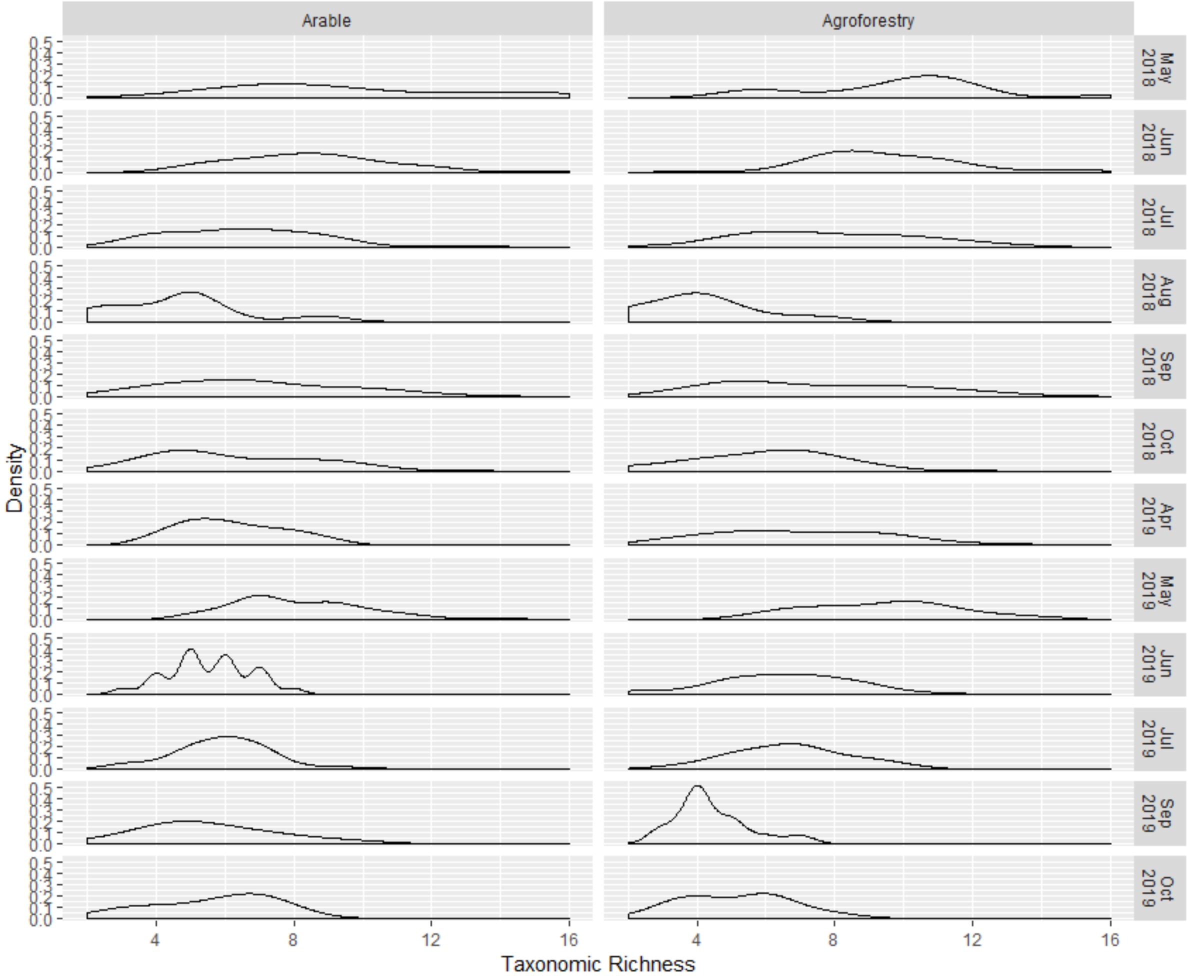


Figure A10.2. Taxonomic richness for herbivores.

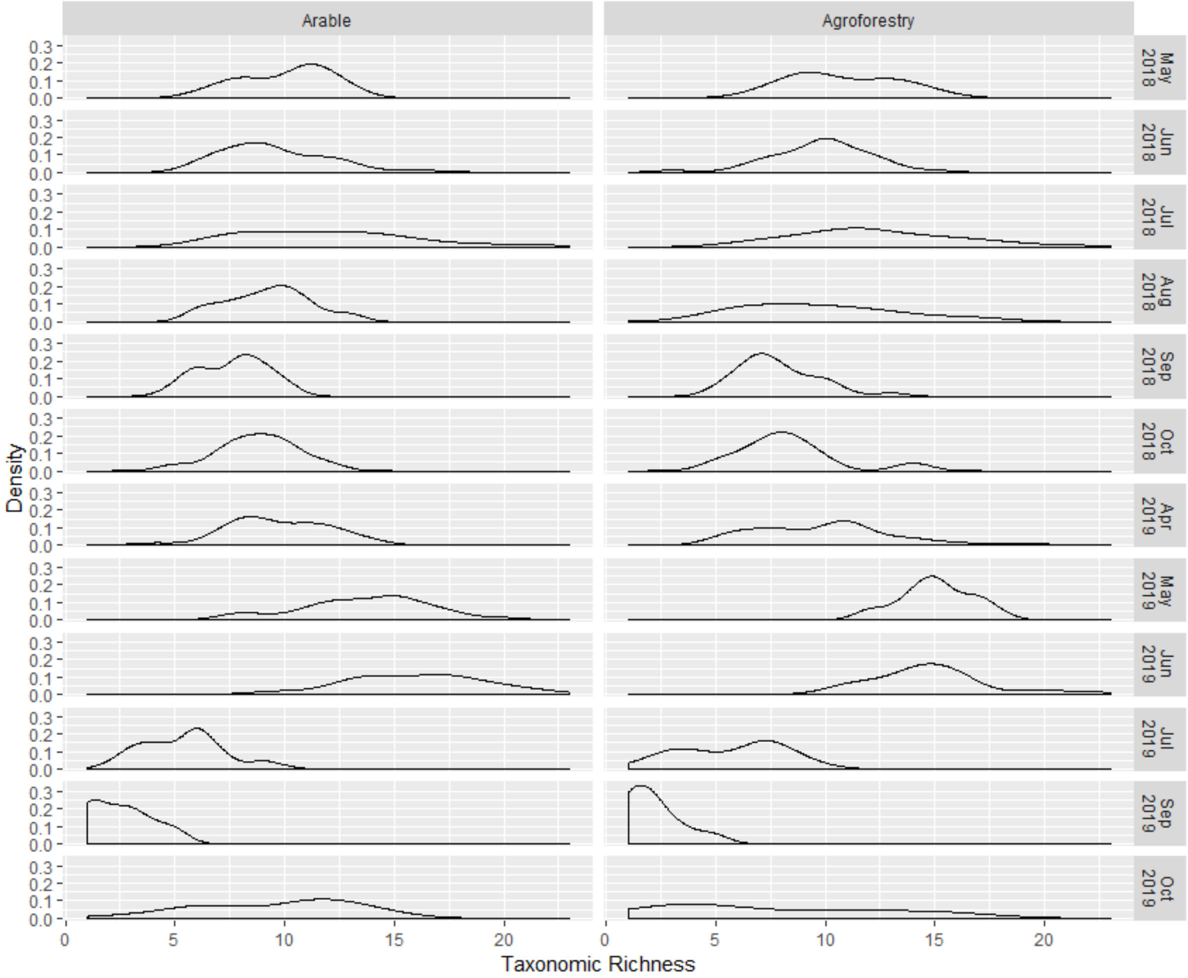


Figure A10.3. Taxonomic richness for natural enemies.

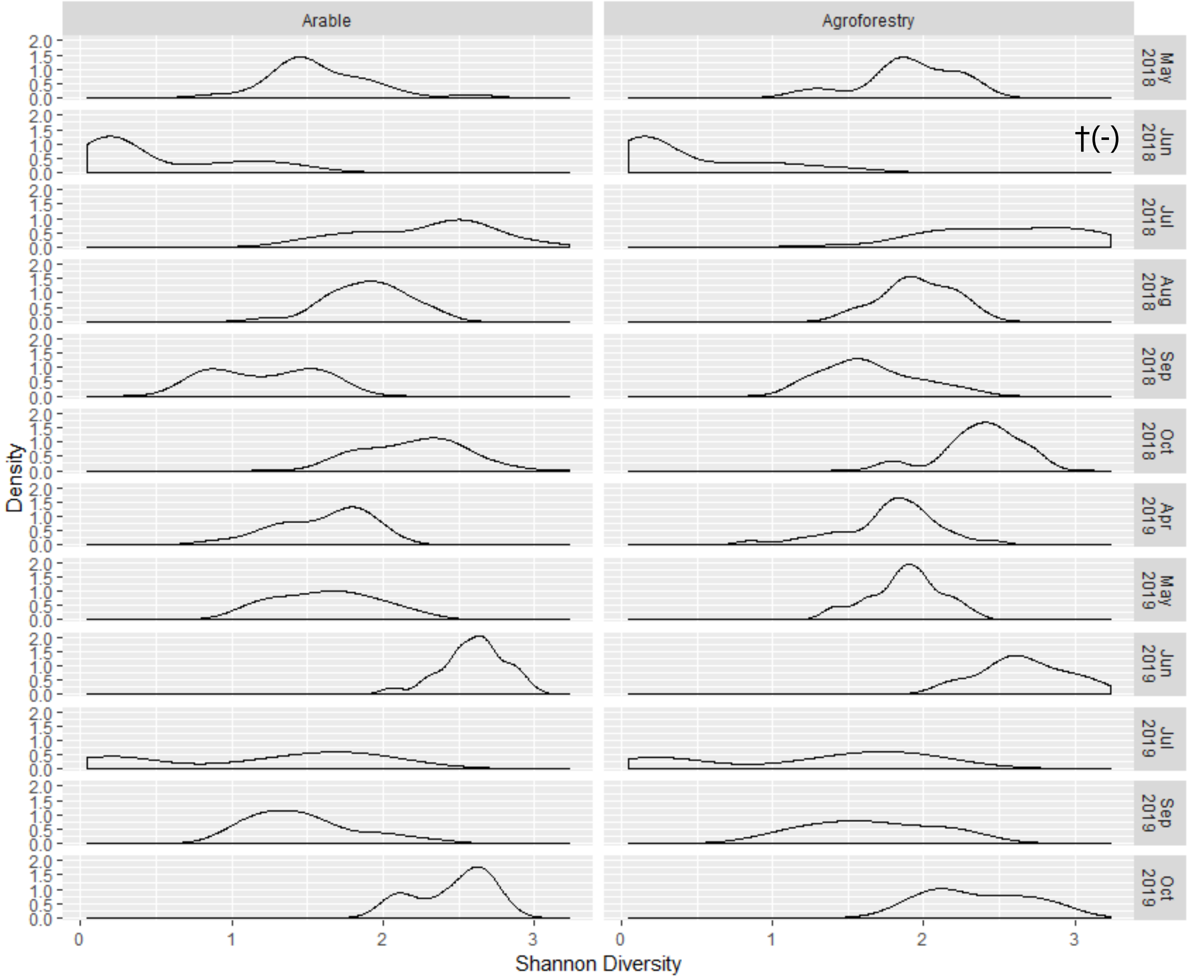


Figure A10.4. Shannon diversity for all invertebrates.

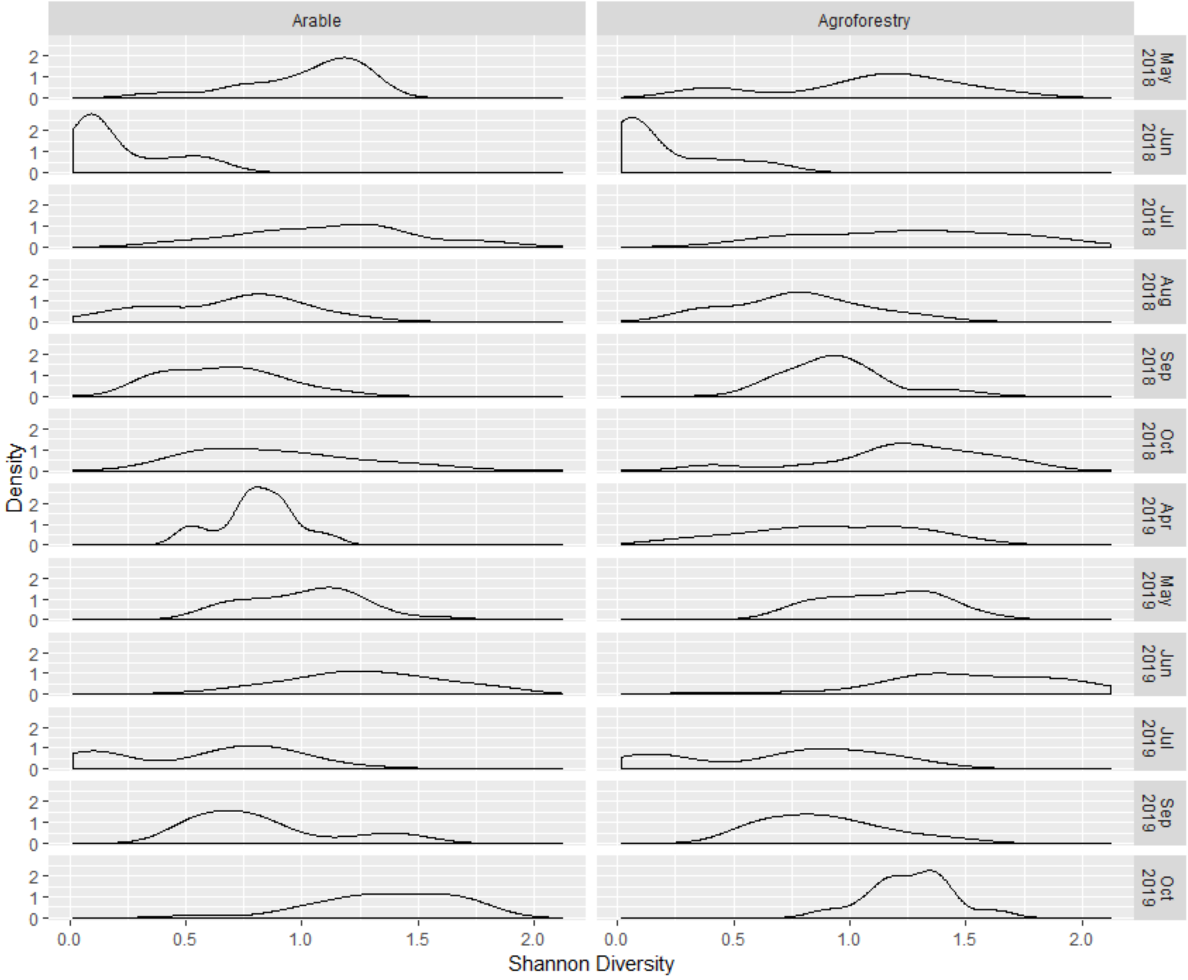


Figure A10.5. Shannon diversity for herbivores.

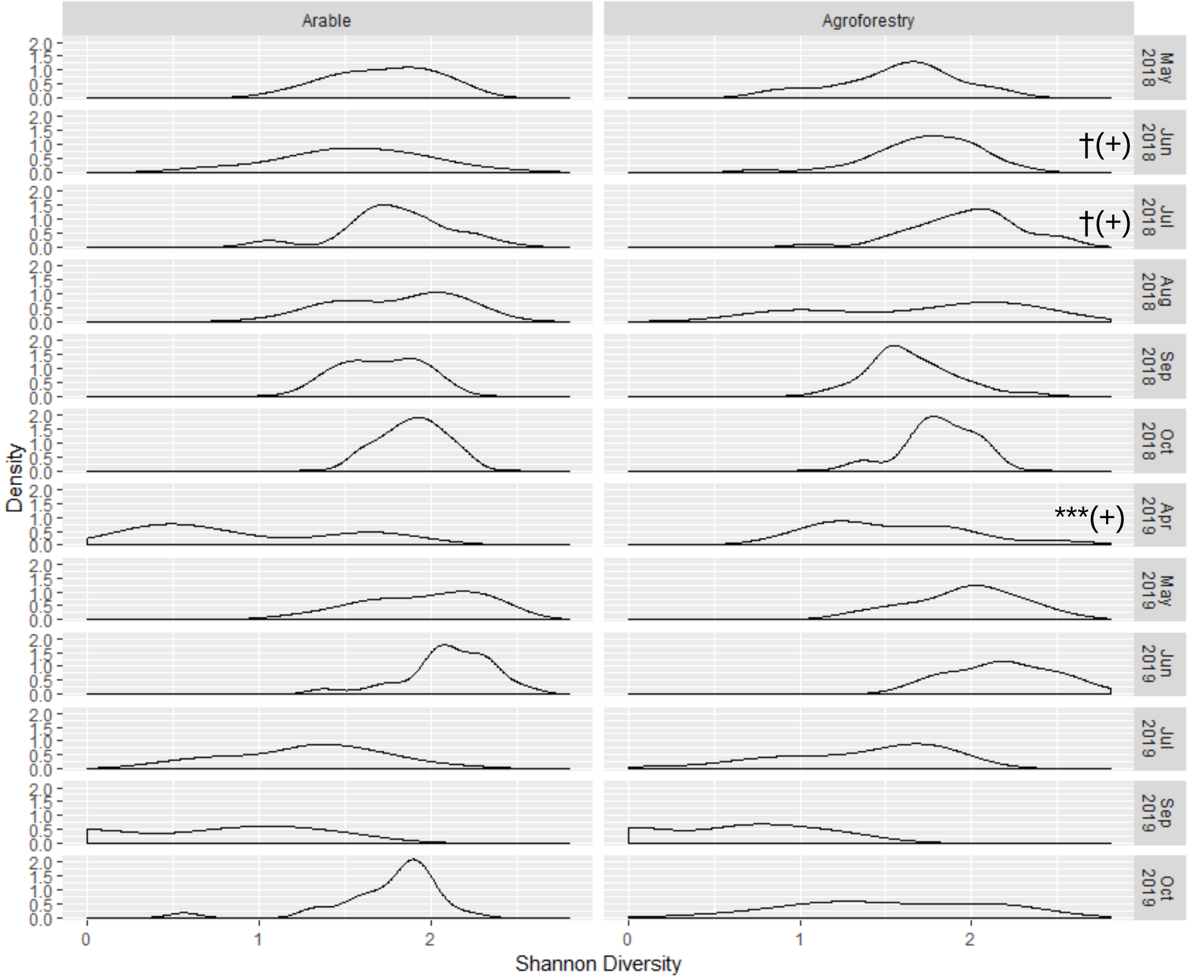


Figure A10.6. Shannon diversity for natural enemies.

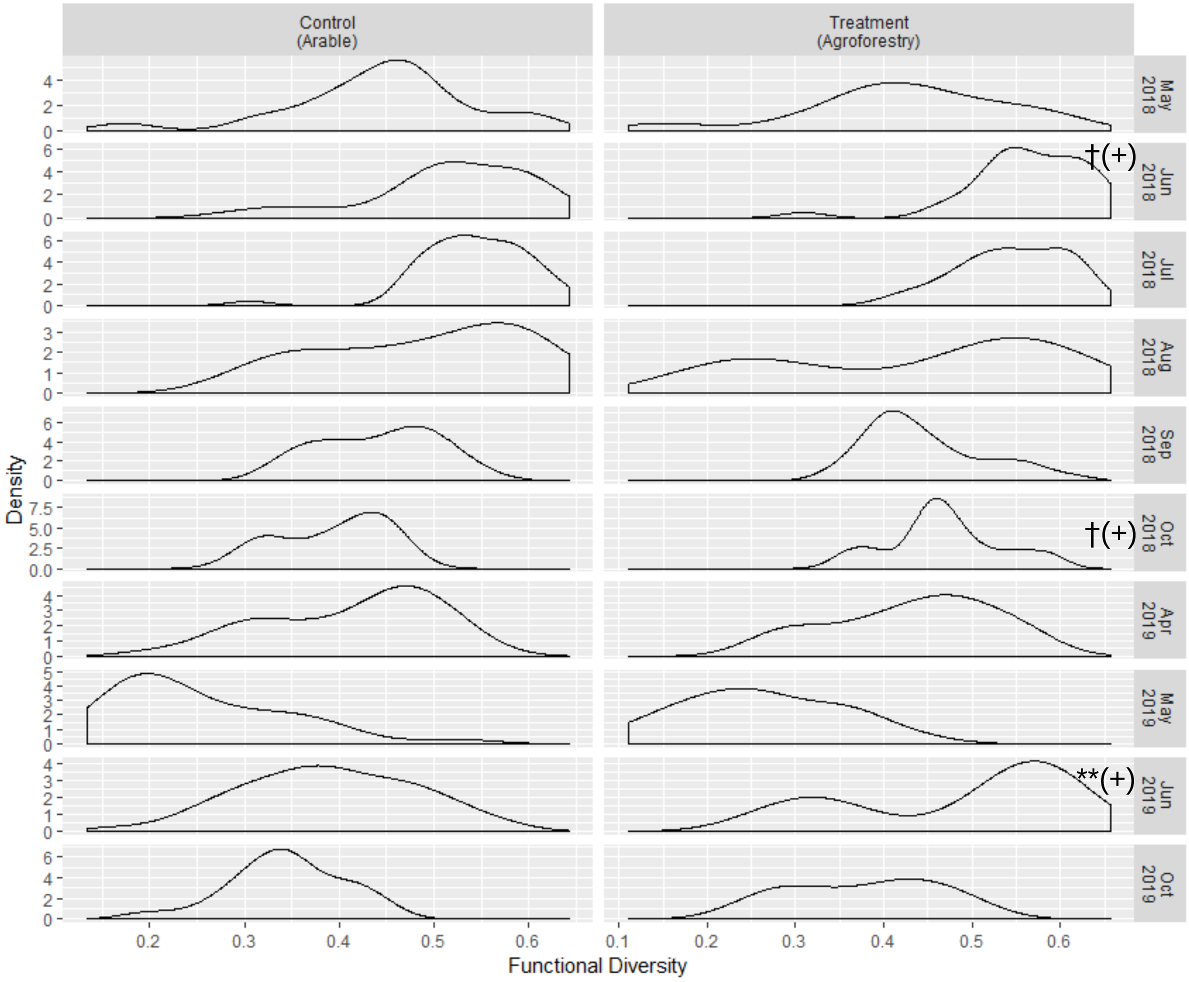


Figure A10.7. Functional trait diversity for natural enemies.

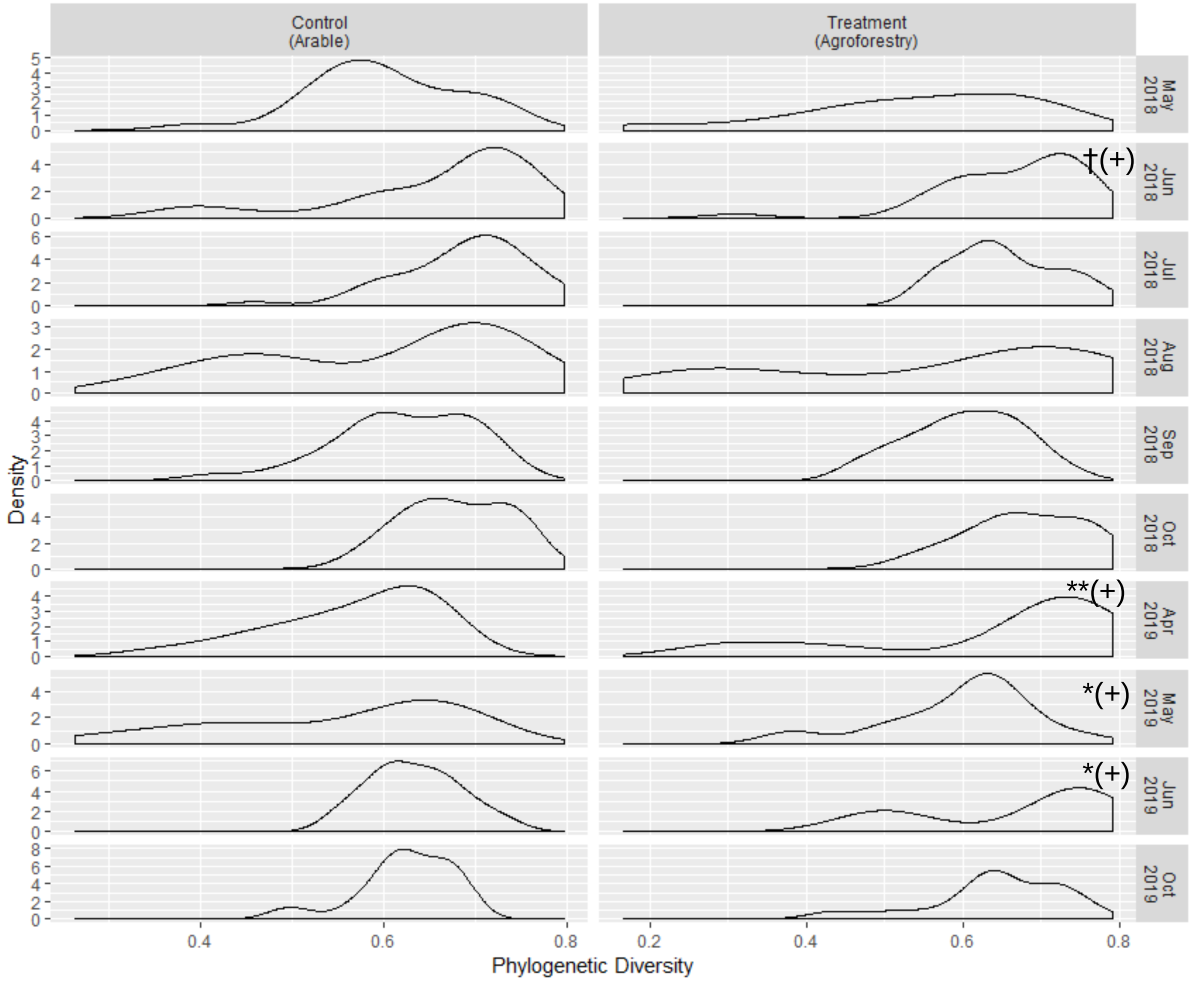


Figure A10.8. Phylogenetic diversity for natural enemies.

8.11 Appendix 11: site-level analysis (Chapter 3)

This appendix sets out a site-level analysis from Chapter 3, comprising outputs of diversity and pest abundance models. Site reference numbers refer to Appendix 3. The single fixed effect was farming system (agroforestry vs arable). Fixed effect estimates above 0 represent positive association with agroforestry relative to arable. Significant results (p-value<0.05) are shown in bold. MM = mixed model, NB = negative binomial, GLMM = Generalized Linear Model.

Taxon / trophic level	**Response variable**	**Site**	**Fixed effect**		**t/z value**	**p-value**	**Model**
			Estimate	**Standard error**			
Diversity metrics							
Plants	Richness	1	**0.567**	**0.267**	**2.122**	**0.039**	MM
		2	0.219	0.257	0.853	0.398	MM
		3	**2.073**	**0.287**	**7.224**	**<0.001**	MM
	Shannon diversity	1	0.202	0.108	1.877	0.067	MM
		2	0.065	0.075	0.865	0.391	MM
		3	**0.527**	**0.090**	**5.838**	**<0.001**	MM
Herbivorous invertebrates	Richness	1	**0.388**	**0.190**	**2.043**	**0.042**	MM
		2	-0.157	0.243	-0.647	0.518	MM
		3	**1.374**	**0.274**	**5.009**	**<0.001**	MM
	Shannon diversity	1	0.071	0.050	1.406	0.161	MM
		2	**0.080**	**0.037**	**2.153**	**0.032**	MM
		3	**0.220**	**0.050**	**4.417**	**<0.001**	MM
Natural enemy invertebrates	Richness	1	0.189	0.446	0.424	0.672	MM
		2	**-1.064**	**0.444**	**-2.398**	**0.017**	MM
		3	**1.241**	**0.598**	**2.073**	**0.039**	MM
	Shannon diversity	1	**0.120**	**0.061**	**1.968**	**0.050**	MM
		2	**-0.139**	**0.040**	**-3.475**	**<0.001**	MM
		3	**0.206**	**0.070**	**2.969**	**0.003**	MM
	Functional diversity	1	**0.019**	**0.009**	**2.130**	**0.035**	MM
		2	**0.040**	**0.011**	**3.748**	**<0.001**	MM
		3	0.012	0.013	0.930	0.354	MM
All invertebrates	Richness	1	0.305	0.523	0.583	0.561	MM
		2	-0.534	0.617	-0.865	0.388	MM
		3	**5.636**	**0.888**	**6.346**	**<0.001**	MM
	Shannon diversity	1	0.085	0.085	1.001	0.318	MM
		2	0.054	0.041	1.296	0.196	MM
		3	**0.334**	**0.068**	**4.929**	**<0.001**	MM
Pests / weeds							
Root flies	Abundance / cover	1	**-0.335**	**0.063**	**-5.301**	**<0.001**	NB GLMM
		2	**-0.407**	**0.082**	**-4.972**	**<0.001**	NB GLMM
		3	**-0.735**	**0.083**	**-8.900**	**<0.001**	NB GLMM
Frit flies		1	-0.038	0.089	-0.421	0.674	NB GLMM
		2	**-0.491**	**0.086**	**-5.685**	**<0.001**	NB GLMM
		3	**0.395**	**0.106**	**3.731**	**<0.001**	NB GLMM

Click beetles / wireworms		1	-2.032	1.049	-1.938	0.053	Poisson GLMM
		2	**0.073**	**0.284**	**5.019**	**<0.001**	Poisson GLMM
		3	-0.484	0.270	-1.791	0.073	Poisson GLMM
Non-crop plant cover		1	N/A (insufficient cover)				
		2	-0.115	0.081	-1.421	0.155	NB GLMM
		3	**0.728**	**0.116**	**6.284**	**<0.001**	NB GLMM
Slugs		1	**0.383**	**0.118**	**3.246**	**0.001**	NB GLMM
		2	**0.492**	**0.133**	**3.694**	**<0.001**	NB GLMM
		3	N/A (insufficient abundance)				

8.12 Appendix 12: understorey plant species

This appendix comprises a list of herbaceous plant species recorded in the tree row understoreys at each site, according to the DAFOR abundance scale (dominant, abundant, frequent, occasional, rare). Years refers to age since establishment of the agroforestry system, and site reference numbers refer to Appendix 3 (Table A3.1) In Chapter 5, only Site 1 was studied.

Species	**Site 1 (5-6 years)**	**Site 2 (4-5 years)**	**Site 3 (8-9 years)**
Achillea millefolium	O	-	-
Alopecurus myosuroides	O	O-D	-
Alopecurus pratensis	-	R	-
Anthriscus sylvestris	-	-	R
Arctium lappa	-	-	R
Arrhenatherum elatius	-	O	O
Artemisia vulgaris	-	R	-
Avena sp.	-	R	F
Bromus hordeaceus	R-O	R-O	F
Bromus sterilis	-	-	A-D
Centaurea nigra	R	-	-
Cirsium arvense	O	O	A-D
Cirsium vulgare	R	R	-
Cynosurus cristatus	R-O	-	-
Dactylis glomerata	R-O	R	-
Daucus carota	R	-	-
Epilobium hirsutum	-	R	-
Epilobium parviflorum	R-O	R-O	-
Epilobium tetragonum	R	R	-
Festuca rubra	D	-	R
Galium aparine	-	-	F-D
Galium verum	R-O	-	-
Geranium dissectum	R	R	-
Geranium molle	-	-	R

Species	**Site 1 (5-6 years)**	**Site 2 (4-5 years)**	**Site 3 (8-9 years)**
Heracleum sphondylium	-	-	R-O
Holcus lanatus	F	O	-
Hordeum brachyantherum	-	O	-
Hordeum murinum	-	-	R
Jacobaea vulgaris	R-O	R	-
Lactuca serriola	-	-	R
Lamium album	-	-	R-O
Leucanthemum vulgare	F-A	-	R-O
Lolium perenne	O	R	-
Lotus corniculatus	O	-	-
Malva moschata	O	-	-
Medicago lupulina	-	R	-
Myosotis arvensis	R	O	-
Papaver rhoeas	-	-	R
Phleum pratense	R-O	F-A	-
Picris echioides	R-F	O-F	-
Plantago lanceolata	-	R	-
Plantago major	R	-	-
Poa trivialis	R-O	A-D	R-O
Prunella vulgaris	O-F	-	-
Ranunculus acris	-	R-F	-
Rubus fruticosus agg.	R	-	-
Rumex conglomeratus	-	R	-
Rumex crispus	-	O	-
Rumex obtusifolius	R	-	R-O
Silene latifolia	O	-	R-O
Sonchus asper	R	-	R
Sonchus oleraceus	-	O	-
Stachys officinalis	-	-	R
Stachys sylvatica	-	-	R
Taraxacum agg.	O	F	-
Trifolium dubium	O	-	-

Species	**Site 1 (5-6 years)**	**Site 2 (4-5 years)**	**Site 3 (8-9 years)**
Trifolium pratense	R	O-D	-
Trifolium repens	O	A	R-O
Triticum sp.	O	-	R
Urtica dioica	-	-	A
Vicia tetrasperma	R-O	-	-

8.13 Appendix 13: abundance, richness and diversity analysis (Chapter 4)

Methods

The effects of farming system (agroforestry versus arable) and position within the agroforestry alley on the abundance of pooled pollinators and three guilds comprising bumblebees, other wild bees, and hoverflies, were analysed using negative binomial generalized linear mixed models (GLMMs) in the R package ‘lme4’ (Bates et al. 2015). Separate models were run for each guild and for each sample method (pan traps and transects). For all models, guild abundance was the response variable, and the explanatory variable was either farming system (agroforestry versus arable), or distance from tree row as a continuous variable. Site was included as a random effect, in addition to month/year for transects. Model assumptions were checked using diagnostic plots. No results are presented for solitary bees recorded on transects, because of the low overall abundance (32, of which 26 were recorded in agroforestry fields), although these were included in the pooled pollinators model. Similarly, no results are presented for bumblebee spatial abundance within agroforestry fields because of their low abundance which caused model convergence issues.

Species richness and Shannon diversity were calculated for each pan trap sample point using the ‘vegan’ package (Oksanen et al. 2013). The effects of (i) farming system and (ii) distance from tree row in the agroforestry fields on richness and diversity were analysed using Poisson GLMMs or linear mixed models, respectively, in the ‘lme4’ package. Separate models were built for bees, hoverflies, and pooled pollinators as response variables. Farming system (agroforestry versus arable) or distance from tree row was the single explanatory variable (in separate models) and site was a random effect.

Results

Guild abundance in agroforestry versus arable

Agroforestry fields yielded 17% more pollinators in pan traps, and 83% more on transects, than arable fields, which were both significant (Table A13.1). At the guild level, pan traps in agroforestry fields captured 164% more bumblebees and 49% more other wild bees than arable fields, while 88% more hoverflies were recorded on transects in agroforestry than arable fields, which were all significant (Table A13.1). Spatial effects within agroforestry fields were only significant for hoverflies in pan traps, which were 27% less numerous at the centre of the alleys compared with tree rows (Table A13.2).

Table A13.1. Negative binomial GLMM outputs for the responses of pollinator guild abundance to farming system (agroforestry versus arable), with site included as a random effect. Positive coefficients represent higher abundance in the agroforestry system.

Guild	**Sample method**	**Farming system coefficient**	**Standard error**	**Z value**	**P-value**	**Marg. R^2**	**Cond. R^2**
Pooled pollinators	Pan	0.157	0.056	2.797	0.005	0.046	0.448
	Transect	0.605	0.223	2.715	0.007	0.037	0.623
Bumblebees	Pan	0.971	0.358	2.716	0.007	0.086	0.116
	Transect	-0.078	0.340	-0.230	0.818	0.029	0.560
Other wild bees	Pan	0.402	0.100	4.012	<0.001	0.129	0.274
Hoverflies	Pan	-0.038	0.063	-0.598	0.550	<0.001	0.815
	Transect	0.630	0.248	2.539	0.011	0.036	0.596

Table A13.2. Negative binomial GLMM outputs for the responses of pollinator guild abundance to distance from agroforestry tree row, with site included as a random effect. Wild bees on transects are not presented separately due to insufficient abundance.

Guild	**Sample method**	**Distance from tree row coefficient**	**Standard error**	**Z value**	**P-value**	**Marg. R^2**	**Cond. R^2**
Pooled pollinators	Pan	<0.001	0.010	0.034	0.973	<0.001	0.420
	Transect	-0.008	0.032	-0.253	0.800	<0.001	0.486
Wild bees	Pan	0.021	0.015	1.358	0.174	0.037	0.034

Hoverflies	Pan	-0.027	0.011	-2.373	0.018	0.029	0.782
	Transect	-0.039	0.033	-1.182	0.237	0.016	0.548

Diversity metrics: agroforestry versus arable

Species richness and Shannon diversity of bees and pooled pollinators were both significantly higher in agroforestry than arable fields (Table A13.3). A mean of 11.65 pollinator species or 6.26 bee species was recorded at each agroforestry pan trap sample point (across all sample visits), compared with 9.65 pollinator or 4.59 bee species in the arable fields. Species richness and Shannon diversity of hoverflies did not significantly differ between farming systems (Table A13.3). There were no significant effects of proximity to tree row in the agroforestry systems on the species richness or Shannon diversity of any group (Table A13.4).

Table A13.3. Outputs of models showing the effect of farming system (agroforestry versus arable) on species richness and diversity. Farming system was the single fixed effect and site was a random effect. Positive coefficients indicate higher values in agroforestry than the arable system.

Metric	**Taxa**	**Model**	**Farming system coefficient**	**SE**	**Z/T value**	**P-value**	**Marg. R^2**	**Cond. R^2**
Species richness	All pollinators	GLMM (poisson)	0.188	0.066	2.846	0.004	0.075	0.227
	Bees		0.309	0.093	3.311	0.001	0.112	0.154
	Hoverflies		0.065	0.094	0.691	0.490	0.004	0.237
Shannon diversity	All pollinators	Mixed model	0.166	0.061	2.721	0.008	0.062	0.282
	Bees		0.241	0.076	3.152	0.002	0.090	0.221
	Hoverflies		0.037	0.078	0.472	0.638	0.002	0.166

Table A13.4. Outputs of models showing the effect of distance from agroforestry tree row on species richness and diversity. Distance from tree row was the single fixed effect and site was a random effect.

Metric	**Taxa**	**Model**	**Distance from tree row coefficient**	**SE**	**Z/T value**	**P-value**	**Marg. R^2**	**Cond. R^2**
Species richness	All pollinators	GLMM (poisson)	<-0.001	0.011	-0.050	0.960	<0.001	0.235
	Bees		0.008	0.015	0.492	0.623	0.005	0.058
	Hoverflies		-0.010	0.017	-0.599	0.549	0.006	0.215
Shannon diversity	All pollinators	Mixed model	0.008	0.009	0.933	0.356	0.011	0.458
	Bees		0.007	0.012	0.540	0.592	0.004	0.381
	Hoverflies		-0.009	0.012	-0.709	0.482	0.009	0.211

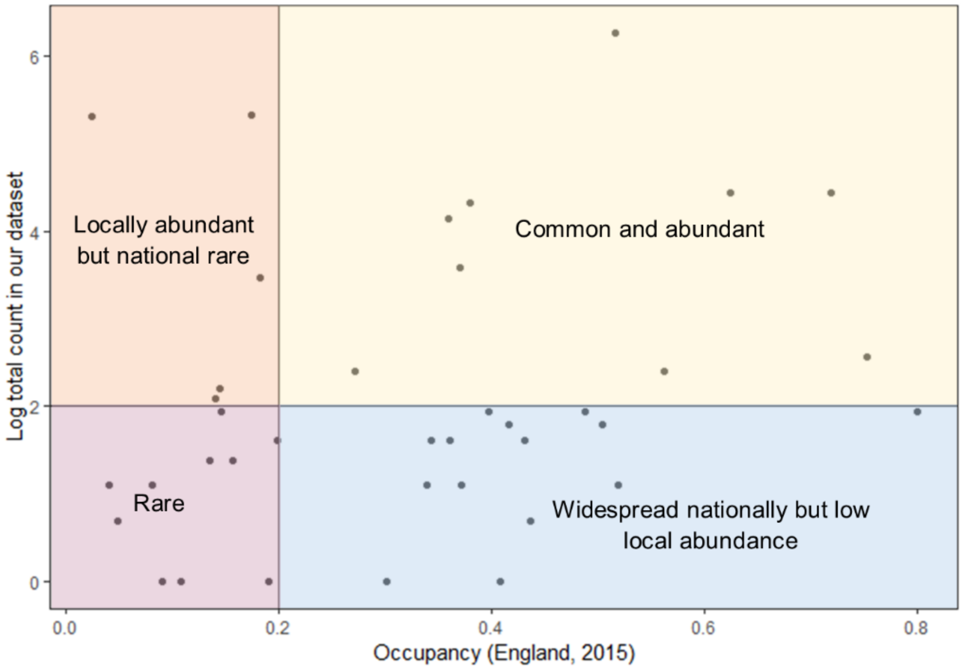
8.14 Appendix 14: response traits (Chapter 4)

This appendix sets out response traits selected for the community analysis of bees and hoverflies.

Taxonomic group	Trait	Trait values and data sources
Bees	Flight period	Number of months of main flight (Falk 2017)
	Tongue (proboscis) length	Continuous variable (mm), predicted using family and intertegular distance (Cariveau et al. 2016; Fortel et al. 2014)
	Sociality	1 = solitary or brood parasite, 2 = primitively eusocial, 3 = eusocial (Falk 2017)
	Voltinism (number of generations)	1 = univoltine, 1.5 = variously uni- or bivoltine, 2 = usually bivoltine (Falk 2017)
	Wing length	Forewing, continuous variable (mm), average within range for species and sex (Falk 2017)
Hoverflies	Duration of development	Number of months of development (egg to puparium), converted to a numeric variable from a categorical variable in Speight et al. (2020) by calculating the mean value in each category, weighted by species association
	Flight period	Number of months of main flight in Britain (Stubbs & Falk 2002)
	Larval diet	Categorical: aphidophagous, phytophagous, or saprophagous (Ball & Morris 2015; Stubbs & Falk 2002)
	Overwintering phase	1 = larva, 2 = puparium, 3 = adult (Speight et al. 2020)
	Voltinism (number of generations)	Converted to a numeric variable from a categorical variable in Speight et al. (2020), as described for ‘duration of development’
	Wing length	Continuous variable (mm), average within range (Stubbs & Falk 2002)

8.15 Appendix 15: bee occupancy versus abundance (Chapter 4)

The figure in this appendix shows the relationship between bee occupancy and abundance. Occupancy was defined in England in 2015 according to Outhwaite et al. (2019). Each point represents a bee species. The four categories indicated by colours broadly illustrate the even spread of species with different occupancy and local abundance. This was confirmed using a linear model (estimate = 1.909, SE = 1.272, t = 1.501, p-value = 0.142).



8.16 Appendix 16: sampling methodology (Chapter 5)

This appendix sets out further information on sample methodology and timings for Chapter 5.

Table A16.1. Sampling methodology. Descriptions of sampling protocol, durations, and limitations.

Sampling method	Protocol for each sample point	Duration of each sample	Summary of main limitations
Visual searches of trees	Each sample tree visually searched for aphid colonies and natural enemies, limited to branches within reach. Particular attention was given to the ends of branches and undersides of leaves.	-	More effective for sedentary rather than mobile (e.g. winged) species.
Visual pest and disease assessment (apples)	Number of apple fruits counted on each tree, then number of fruits damaged by scab or insect pests counted, based on appearance of fruit. Observed insect pest damage included substantially stunted fruit size due to aphid feeding, codling moth, winter moth, blastobasis moth, sawfly. Entire tree sampled for aphids, five branches per tree haphazardly selected for other pests and scab.	-	-
Flower visitation counts	Timed counts of 3 minutes per sample tree, pollinator visitation to apple flowers counted, avoiding multiple counts for the same insect. Undertaken during favourable weather conditions Only undertaken during suitable weather conditions, i.e. maximum temperature of at least 13 ˚C, maximum wind speed less than 25 mph, and no rain. Entire sample tree observed.	3 minutes	Can lead to overestimation if pollinators re-visit the tree, especially when activity is high.
Apple seed counts, fruit count and width	Four apples haphazardly selected from each sample tree. Maximum width and number of seeds measured for each fruit. Seed count responds to pollination level (Webber et al. 2020). Number of fruits per sample tree counted pre-harvest to estimate yield.	-	-

Pitfall traps	Plastic cup, 70 mm diameter x 100 mm depth. Wire mesh (30 mm) fitted over top to prevent mammal captures. Trapping fluid: 60ml of propylene glycol solution diluted to 50% concentration, with small amount of scentless detergent. Increased to 90ml at 33% concentration in warm dry conditions. Of the 200 pitfall trap samples, three were damaged and no sample could be collected.	7 or 8 days	Capture rates reflect both abundance and activity, therefore they are a measure of activity-density rather than abundance. Vegetation structure can influence capture rate (Lang 2000; Woodcock 2005).
Sticky traps	Yellow sticky traps, 100 mm x 250 mm (Agrigem Ltd, Lincoln, UK). Set horizontally and raised above ground by approx. 250 mm on bamboo skewers. Only undertaken during suitable weather conditions (as for flower visitation counts).	7 hours	As with UV water traps, attraction to colours varies among species. In addition, abundant floral resources can reduce capture rates by reducing searching activity (O'Connor et al. 2019).
Grain samples	Sample taken from 50 x 50 cm quadrat, within one week of the field harvest commencing, after a period of warm dry weather. Samples were threshed using a Wintersteiger Hege 16 and then weighed.	-	-

Table A16.2. Timings of sampling and management activities. Each number represents the date (or date range) the activity was carried out within the corresponding month.

Sampling or management activity	Nov 2019	Apr 2020	May 2020	Jun 2020	Jul 2020	Aug 2020	Sep 2020
Visual searches		24	2 9 27	4 24	1 21		
Apple pest and disease assessment					28		5 (aphid damage)
Flower visitation		24	2 9 (Block 4 only)				
Apple seed counts and yield estimates							12
Pitfall trapping			2-9 27-	-4 24-	-1 21-28		5-12
Sticky trapping			27	24	21		
Grain samples						15	
Understorey mowing	10	24	9	4	1 28		

8.17 Appendix 17: model outputs and block-level analysis (Chapter 5)

This appendix sets out model outputs from Chapter 5, in addition to analyses broken down by sample block to facilitate an evaluation of the influence of individual blocks on the overall results. In all cases, the unmown flowering understoreys were the ‘treatment’ and mown understoreys were the ‘control’, hence, positive estimated regression parameters represent association with flowering understoreys.

Table A17.1. Block-level analysis: mean abundance and standard error of aphid colonies, pollinator visitation, and thrips in each sample block.

Sample block	**Mean in flowering**	**Std. error in flowering**	**Mean in mown**	**Std. error in mown**
Aphid colony abundance in apple trees (log(x+1) transformed)				
1	0.475	0.087	0.704	0.132
2	0.558	0.123	0.423	0.099
3	0.628	0.135	0.943	0.142
4	0.541	0.104	0.558	0.114
5	0.457	0.119	0.943	0.125
Pollinator visitation to apple flowers (log(x+1) transformed)				
1	1.018	0.195	1.024	0.254
2	1.434	0.326	1.286	0.344
3	0.704	0.293	0.571	0.187
4	0.971	0.162	0.554	0.133
5	0.808	0.254	0.448	0.178
Abundance of thrips (Thysanoptera) in crop alleys				
1	27.250	5.018	35.083	3.844
2	25.333	4.794	43.500	5.625
3	23.750	4.338	29.500	2.726
4	25.000	4.086	25.667	6.550
5	25.583	2.681	28.083	4.186

Table A17.2. Model outputs for natural enemies and aphids in apple trees: outputs of Poisson GLMMs testing the effect of understorey management on abundance of natural enemies and aphids.

Fixed effect	**Estimate**	**Std. error**	**z value**	**p-value**
Natural enemies (marginal R^2=0.197, conditional R^2=0.203)				
Treatment:visit 1	0.629	0.438	1.438	0.150
Treatment:visit 2	1.224	0.508	2.407	0.016
Treatment:visit 3	-0.032	0.464	-0.686	0.493
Treatment:visit 4	<0.001	0.577	<0.001	0.999

Treatment:visit 5	0.305	0.352	0.867	0.386
Treatment:visit 6	-0.938	0.393	-2.388	0.017
Treatment:visit 7	-0.182	0.303	-0.603	0.547
Treatment:visit 8	-0.493	0.271	-1.821	0.069
Aphid colonies (marginal R^2=0.497, conditional R^2=0.537)				
Treatment:visit 1	-0.788	0.538	-1.465	0.143
Treatment:visit 2	-0.163	0.329	-0.494	0.622
Treatment:visit 3	-0.266	0.277	-0.960	0.337
Treatment:visit 4	-0.464	0.204	-2.273	0.023
Treatment:visit 5	-0.250	0.155	-1.614	0.106
Treatment:visit 6	-0.693	0.306	-2.268	0.023
Treatment:visit 7	-0.833	0.378	-2.203	0.028
Treatment:visit 8	-0.154	0.555	-0.278	0.781

Table A17.3. Diversity model outputs: outputs of mixed models testing effect of understorey management on Shannon diversity and richness of different trophic levels in pitfall traps.

Fixed effect	**Estimate**	**Std. error**	**Df**	**T value**	**p-value**
All invertebrates – Shannon diversity (marginal R^2=0.176, conditional R^2=0.202)					
Treatment:visit 1	0.137	0.057	183	2.421	0.016
Treatment:visit 2	0.164	0.056	183	2.933	0.004
Treatment:visit 3	0.074	0.056	183	1.319	0.189
Treatment:visit 4	-0.008	0.057	183	-0.143	0.887
Treatment:visit 5	-0.038	0.056	183	-0.673	0.502
All invertebrates – richness (marginal R^2=0.155, conditional R^2=0.193)					
Distance from boundary	-0.026	0.009	5	-3.012	0.030
Treatment:visit 1	2.164	1.122	183	1.929	0.055
Treatment:visit 2	2.373	1.107	183	2.143	0.033
Treatment:visit 3	1.623	1.107	183	1.466	0.144
Treatment:visit 4	0.543	1.137	183	0.478	0.633
Treatment:visit 5	-0.927	1.107	183	-0.837	0.404
Herbivores – Shannon diversity (mixed model, marginal R^2=0.118, conditional R^2=0.118)					
Treatment:visit 1	0.182	1.116	187	1.566	0.119
Treatment:visit 2	-0.022	1.114	187	-0.188	0.851
Treatment:visit 3	0.122	1.114	187	1.063	0.289
Treatment:visit 4	0.127	1.117	187	1.078	0.282
Treatment:visit 5	-0.064	1.114	187	-0.562	0.575
Herbivores – richness (marginal R^2=0.124, conditional R^2=0.124)					
Distance from boundary	-0.005	0.002	186	-2.231	0.027
Treatment:visit 1	0.511	0.477	186	1.072	0.285
Treatment:visit 2	-0.035	0.470	186	-0.075	0.940
Treatment:visit 3	0.865	0.470	186	1.838	0.068
Treatment:visit 4	0.718	0.483	186	1.488	0.139
Treatment:visit 5	-0.135	0.470	186	-0.288	0.774
Natural enemies – Shannon diversity (marginal R^2=0.188, conditional R^2=0.193)					
Distance from boundary	-0.001	0.0004	3.947	-3.352	0.029
Treatment:visit 1	0.156	0.068	183	2.282	0.024

Treatment:visit 2	0.168	0.067	183	2.494	0.014
Treatment:visit 3	0.035	0.067	183	0.519	0.605
Treatment:visit 4	-0.123	0.069	183	-1.772	0.078
Treatment:visit 5	-0.032	0.067	183	-0.472	0.637
Natural enemies – richness (marginal R^2=0.140, conditional R^2=0.193)					
Distance from boundary	-0.016	0.006	5.78	-2.539	0.046
Treatment:visit 1	1.614	0.736	183	2.192	0.030
Treatment:visit 2	1.894	0.726	183	2.607	0.010
Treatment:visit 3	0.494	0.726	183	0.680	0.497
Treatment:visit 4	-0.522	0.746	183	-0.700	0.485
Treatment:visit 5	-0.356	0.726	183	-0.490	0.625

Table A17.4. Block-level analysis for natural enemy diversity: mean values with standard errors (in brackets) for Shannon diversity and richness of natural enemies in pitfall traps in April and May, in each sample block.

Sample block	**Diversity in flowering**	**Diversity in mown**	**Richness in flowering**	**Richness in mown**
April 2020				
1	2.231 (0.076)	2.050 (0.078)	12.75 (0.946)	11.5 (1.708)
2	1.754 (0.041)	1.877 (0.057)	10.0 (0.913)	10.0 (0.577)
3	2.399 (0.081)	1.883 (0.050)	16.0 (2.614)	10.25 (0.250)
4	2.211 (0.072)	1.968 (0.087)	13.25 (0.479)	12.25 (0.479)
5	1.847 (0.207)	1.906 (0.081)	10.75 (1.931)	11.0 (1.581)
May 2020				
1	2.029 (0.129)	1.995 (0.166)	12.25 (1.181)	10.5 (1.555)
2	1.939 (0.046)	1.785 (0.136)	11.0 (0.913)	10.5 (1.658)
3	2.076 (0.045)	1.766 (0.096)	13.25 (0.629)	9.0 (1.826)
4	2.071 (0.054)	1.950 (0.052)	12.75 (0.629)	12.5 (0.500)
5	2.059 (0.077)	1.852 (0.102)	12.75 (1.377)	10.25 (1.181)

Table A17.5. Model outputs for sticky traps: outputs of mixed models testing the effect of understorey management on Shannon diversity and richness of different trophic levels in sticky traps.

Fixed effect	**Estimate**	**Std. error**	**Df**	**T value**	**p-value**
All invertebrates – Shannon diversity (marginal R^2=0.725, conditional R^2=0.765)					
Treatment:visit 1	-0.067	0.060	110	-1.120	0.265
Treatment:visit 2	0.085	0.060	110	1.420	0.158
Treatment:visit 3	0.071	0.060	110	1.183	0.240
All invertebrates – richness (marginal R^2=0.406, conditional R^2=0.484)					
Treatment:visit 1	-0.150	0.737	110	-0.204	0.839
Treatment:visit 2	-0.200	0.737	110	-0.271	0.787
Treatment:visit 3	-0.250	0.737	110	-0.339	0.735
Herbivores – Shannon diversity (marginal R^2=0.436, conditional R^2=0.515)					
Treatment:visit 1	-0.110	0.081	110	-1.358	0.177
Treatment:visit 2	0.128	0.081	110	1.581	0.117

Treatment:visit 3	0.019	0.081	110	0.239	0.811
Herbivores – richness (marginal R^2=0.320, conditional R^2=0.399)					
Treatment:visit 1	-0.500	0.412	110	-1.212	0.228
Treatment:visit 2	0.200	0.412	110	0.485	0.629
Treatment:visit 3	-0.350	0.412	110	-0.849	0.398
Natural enemies – Shannon diversity (marginal R^2=0.209, conditional R^2=0.296)					
Treatment:visit 1	0.052	0.103	110	0.509	0.612
Treatment:visit 2	0.091	0.103	110	0.879	0.381
Treatment:visit 3	-0.051	0.103	110	-0.500	0.618
Natural enemies – richness (marginal R^2=0.288, conditional R^2=0.346)					
Treatment:visit 1	0.150	0.368	110	0.408	0.684
Treatment:visit 2	0.450	0.368	110	1.224	0.224
Treatment:visit 3	0.100	0.368	110	0.272	0.786

Table A17.6. Model outputs for pest abundance: effects of understorey treatment on pest abundance according to negative binomial GLMMs.

Taxon	**Sampling method**	**Estimate**	**Standard error**	**z value**	**p-value**	**R^2 marginal**	**R^2 conditional**
Root flies (Anthomyiidae)	Pitfall traps	0.068	0.137	0.494	0.621	0.001	0.248
Wheat stem sawfly (*Cephus*)	Sticky traps, visit 1	-0.043	0.180	-0.238	0.812	0.001	0.001
Aphids (Aphididae)	Sticky traps, visits 1 & 2	-0.229	0.149	-1.542	0.123	0.021	0.159
Frit flies (Chloropidae)	Sticky traps	-0.280	0.162	-1.725	0.084	0.009	0.751
Thrips (Thysanoptera)	Sticky traps	-0.282	0.097	-2.912	0.004	0.054	0.265
Slugs (*Arion* spp. and *Deroceras reticulatum*)	Pitfall traps, visits 1,3,4	-0.111	0.246	-0.450	0.653	<0.001	0.085

8.18 Appendix 18: alternative apple price scenario (Chapter 5)

This appendix describes an alternative pricing scenario for our financial model, comprising a hypothetical eating / cooking fruit market rather than the heritage juice market described in the Chapter 5.

Methodology

Under the alternative apple price scenario, the same formulae and parameters other than apple price (AP) were applied as described in Section 5.3.4. National average prices for 2018 to 2020 were sourced from Defra (2021), applying Bramley's Seedling price of £1,180.87/t to cooking apples (Lord Derby and Bramley's Seedling) and 'other late season' price of £947.83/t to the other three varieties. Prices in 2020 were substantially higher than in 2018 and 2019 for the cooking apple price (but not the 'other late season' price). Such high prices could persist depending on the long-term economic impacts of the UK's departure from the EU. Defra prices are an average of Class 1 and 2, which is likely to result in an underestimate of our total crop values, because 75% of the apples in our dataset were Class 1 (based on maximum width of >60 mm for eating or >80 mm for cooking apples). Variable costs of £376.80/t were subtracted, to account for harvesting, packing, transport, and commission (Redman 2017). The proportion of apples damaged by other pests and scab was removed from this price scenario, which accounted for between 5.3 and 11.8 % of fruits, depending on variety and treatment.

Results

Under the alternative price scenario, flowering understoreys increased farm income by a mean of £167.99 per ha of agroforestry, compared with mown understoreys (Table A18.1).

Table A18.1. Predicted changes in income (£/ha of agroforestry) arising from using a flowering understorey relative to a mown understorey, applying an alternative price scenario comprising mean national average prices for eating and cooking apples (2018-2020). Positive values represent higher income (or less cost) from using the flowering understorey. Flower mix grants are for Countryside Stewardship AB8. The 'Spartan' block results should be interpreted with caution, because aphid damage was very low (< 1%). u/s = understorey.

Apple variety	**Predicted increase in income from reduced apple yield loss to aphids**	**Income from flower mix grant**	**Reduction in mowing costs**	**Total predicted increase in income from flowering u/s relative to mown u/s**
Lord Derby	370.39	53.90	13.50	437.79
Spartan	-5.31			62.09
King of the Pippins	-14.32			53.08
Bramley's Seedling	107.92			175.32
D'Arcy Spice	44.26			111.66
Mean	100.59	53.90	13.50	167.99

8.19 Appendix 19: calculation of apple weights (Chapter 5)

To determine the relationship between apple width and weight, data was sourced from Garratt et al. (2016b), which contains weight and width metrics for two apples varieties (Bramley and Braeburn) measured from three sites in Kent, UK. The relationship between weight and width was visually explored, and weight was log-transformed to improve linearity. A mixed model was fitted to this dataset using the ‘lme4’ package in R (Bates et al. 2015; R Core Team 2018), where log-transformed apple weight was the response variable, apple width was the explanatory variable, and site was a random effect. The relationship between width and weight was highly statistically significant (p-value < 0.001). We then derived predicted apple weights for each fruit in our dataset based on measured widths, using the ‘predict’ function in R.

8.20 Appendix 20: photos of understorey managements (Chapter 5)

The following photos show understorey management treatments over the season in 2020. Mown treatments are shown on the left, unmown ‘flowering’ on the right.

23 April 2020

27 May 2020

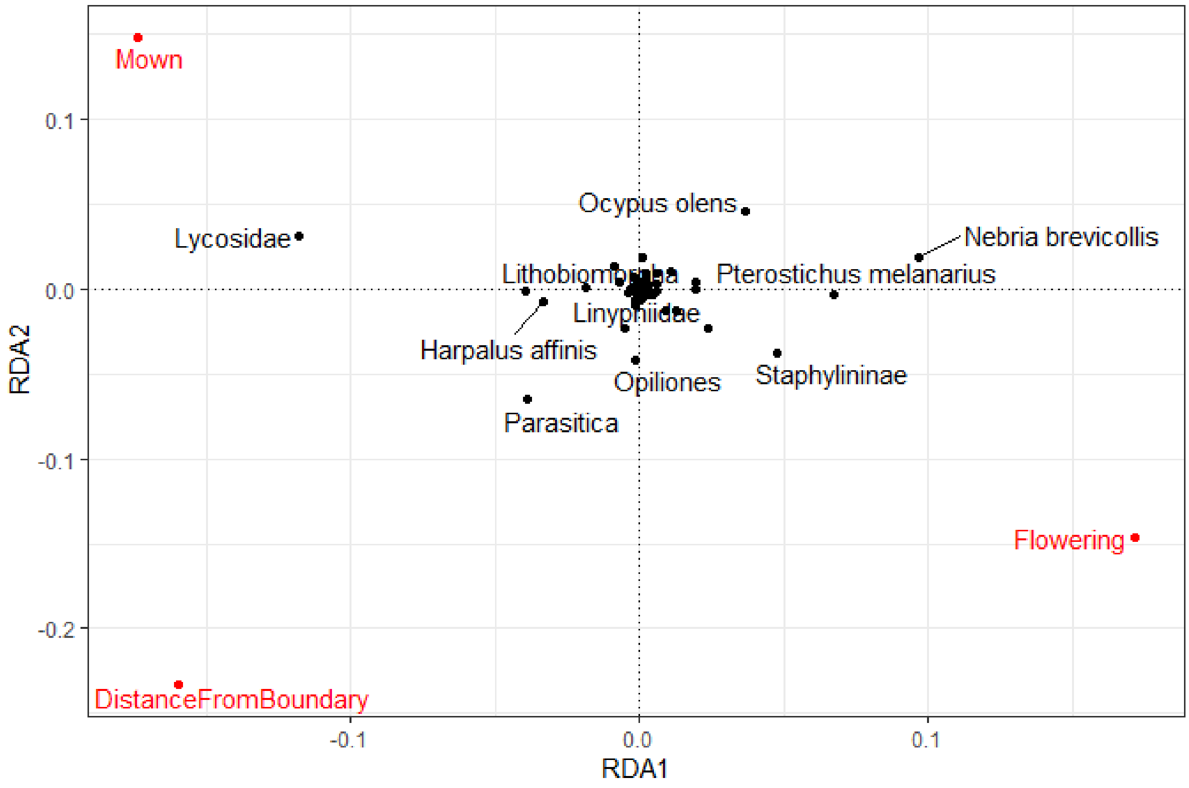
23 June 2020

21 July 2020

12 September 2020

8.21 Appendix 21: effects of understorey management and distance from boundary on natural enemies (Chapter 5)

This appendix sets out the outcome of a redundancy analysis showing the effect of understorey management and distance from boundary (in red) on natural enemy taxa (in black) captured in pitfall traps in adjacent crop alleys, according to partial redundancy analysis (F = 1.458, p-value = 0.089). Sample block and visit were 'partialled out' covariables. Only the ten most abundant taxa are labelled.



8.22 Appendix 22: methods for predicting apple weight and pollination valuation (Chapter 6)

Calculation of predicted apple weights from width measurements.

To determine the relationship between apple width and weight, data was sourced from Garratt et al. (2016b), which contains weight and width metrics for two apples varieties (Bramley and Braeburn) measured from three sites in Kent, UK. The relationship between weight and width was visually explored, and weight was log-transformed to improve linearity. A mixed model was fitted to this dataset using the 'lme4' package in R (Bates et al. 2015; R Core Team 2018), where log-transformed apple weight was the response variable, apple width was the explanatory variable, and site was a random effect. The relationship between width and weight was highly statistically significant ($p<0.001$). We then derived predicted apple weights for each fruit in our dataset based on measured widths, using the 'predict' function in R.

Pollination valuation

Pollination valuation followed a two-stage process. Firstly, we estimated apple width, weight and fruit set for all apples in the dataset using seed counts, based on relationships for each variety (Braeburn and Bramley) in Garratt et al. (2016b). This approach allowed us to control for confounding variables, such as soil, climate and management, that could affect width, weight and fruitset.

Secondly, using this predicted data we adapted formulae from Garratt et al. (2014) to compare financial outputs of agroforestry and orchard systems per hectare of apples, for each variety (Equation 1). Six scenarios were separately tested, based on organic management and production level (Table A22.1). In each scenario, organic management was the same for both farming systems, e.g. the comparison between agroforestry and conventional orchards assumed conventional values for both, to isolate the influence of seed set on financial output.

Table A22.1. Parameterisation of economic valuation scenarios. Values were derived from Farm Management Handbooks (Lampkin et al. 2017; Redman 2017). All figures are per tonne of apples. Financial figures are in Euros. Conventional yields were adjusted for tree density in agroforestry. Prices were based on dessert apples, because recent Bramley apple prices are similar to dessert apples (Defra 2021), and to improve the comparability of the two varieties. Cost of production refers to harvest costs as set out in Appendix 26.

Scenario	**Price (*P*)**	**Cost of production per tonne (*C*)**	**Yield (*Y*)**
Conventional, low production	872.02	444.62	14.55
Conventional, average production	872.02	444.62	23.91
Conventional, high production	872.02	444.62	33.27
Organic, low production	1416	519.40	2
Organic, average production	1416	519.40	16
Organic, high production	1416	519.40	26

$$(1)\ PV_c = V_{cAF} - V_{cO} \times A$$

Where PV_c is the difference in economic output in cultivar c between agroforestry and orchard systems, V_{cAF} is the economic output of cultivar c in agroforestry (Equation 2), V_{cO} is the equivalent value for orchards, and *A* is the area of agroforestry occupied by fruit trees, assumed to be 9.2%. Economic outputs for each farming system were calculated as:

$$(2)\ V_{cT} = (P \times O_{cT}) - (O_{cT} \times C)$$

Where V_{cT} represents economic output for cultivar *c* in farming system *T* (agroforestry or arable), *P* represents the price, O_{cT} represents the quantity of apples in treatment *T* (Equation 3), and *C* represents the cost of production per tonne of apples, such as harvesting costs.

$$(3)\ O_{cT} = Y \times S_{cT} \times W_{cT}$$

Where *Y* represents expected yield, S_{cT} is the change in percentage fruitset compared with the orchard system (i.e. agroforestry fruit set divided by orchard fruit set, or 1 where *T* = orchard), and W_{cT} is the change in mean weight compared with the orchard system (i.e. agroforestry mean weight divided by orchard mean weight, or 1 where T = orchard). Fruit set, weight and width were predicted from seed numbers, as set out above. All apples were assumed to be Class 1, because the minimum estimated apple width was greater than 60 mm and 80 mm for Braeburn and Bramley respectively, for both farming systems.

8.23 Appendix 23: model outputs (Chapter 6)

This appendix sets out model outputs from Chapter 6. Each table represents a separate model. In all cases, the monoculture control (arable or orchard) was the reference level for farming system.

Table A23.1. Mixed model output for Grain weight ~ farming system * crop type, with main effect for farming system removed. Barley/Wheat is the reference level for crop type. Marginal R^2 = 0.046, conditional R^2 = 0.820.

Fixed effect	Estimate	SE	df	t value	P-value
Intercept	5.377	1.864	2.683	2.885	0.072
Crop	1.701	1.824	2.303	0.933	0.438
Farming system:Oats	-0.029	0.334	144	-0.087	0.931
Farming system: BarleyWheat	-0.809	0.331	144	-2.440	0.016

Table A23.2. Mixed model output for Grain weight ~ distance from tree row, subset for the agroforestry data only. Marginal R^2 = 0.009, conditional R^2 = 0.817.

Fixed effect	Estimate	SE	df	t value	P-value
Intercept	5.470	1.508	1.984	3.626	0.069
Distance from tree row	0.082	0.046	62	1.796	0.077

Table A23.3. Mixed model output for Grain weight ~ farming system + weed cover + slug abundance. Marginal R^2 = 0.077, conditional R^2 = 0.734.

Fixed effect	Estimate	SE	df	t value	P-value
Intercept	8.785	1.360	2.242	6.458	0.017
Farming system	0.050	0.280	110.665	0.180	0.857
Weed cover	-0.020	0.006	86.807	-3.045	0.003
Slug abundance	-0.174	0.097	72.888	-1.798	0.076

Table A23.4. Mixed model output for Grain weight ~ farming system * weed cover. Marginal $R^2 = 0.057$, conditional $R^2 = 0.705$.

Fixed effect	**Estimate**	**SE**	**df**	**t value**	**P-value**
Intercept	8.337	1.314	2.520	6.343	0.013
Farming system	0.270	0.457	110.115	0.592	0.555
Weed cover	-0.016	0.008	110.151	-2.026	0.045
Farming system: Weed cover	-0.007	0.009	110.238	-0.794	0.429

Table A23.5. Mixed model output for Grain weight ~ farming system * slug abundance. Marginal $R^2 = 0.017$, conditional $R^2 = 0.785$.

Fixed effect	**Estimate**	**SE**	**df**	**t value**	**P-value**
Intercept	8.223	1.673	2.380	4.914	0.027
Farming system	-0.314	0.356	110.340	-0.881	0.380
Slug abundance	-0.275	0.151	108.561	-1.818	0.072
Farming system: Slug abundance	0.130	0.149	110.748	0.872	0.385

Table A23.6. Binomial GLMM model output for Seed count ~ Year (as factor) for Braeburn orchard data. Theoretical marginal $R^2 = 0.004$, conditional $R^2 = 0.067$.

Fixed effect	**Estimate**	**SE**	**z value**	**P-value**
Intercept	-0.490	0.419	-1.171	0.242
Year	-0.236	0.584	-0.403	0.687

Table A23.7. Binomial GLMM model output for Seed count ~ Year (as factor) for Bramley orchard data. Theoretical marginal $R^2 = 0.022$, conditional $R^2 = 0.022$.

Fixed effect	**Estimate**	**SE**	**z value**	**P-value**
Intercept	-2.135	0.319	-6.695	<0.001
Year	0.562	0.460	1.223	0.221

Table A23.8. Binomial GLMM model output for Seed count ~ Farming system for Braeburn. Theoretical marginal R^2 = 0.002, conditional R^2 = 0.084.

Fixed effect	**Estimate**	**SE**	**z value**	**P-value**
Intercept	-0.619	0.323	-1.918	0.056
Farming system	-0.154	0.539	-0.286	0.775

Table A23.9. Binomial GLMM model output for Seed count ~ Farming system for Bramley. Theoretical marginal R^2 = 0.022, conditional R^2 = 0.022.

Fixed effect	**Estimate**	**SE**	**z value**	**P-value**
Intercept	-1.893	0.229	-8.275	<0.001
Farming system	0.570	0.270	2.108	0.035

Table A23.10. Binomial GLMM model output for Seed count ~ Farming system + pesticide use (as a binary factor) for Braeburn. Conventional pesticide use was the reference level. Theoretical marginal R^2 = 0.006, conditional R^2 = 0.084.

Fixed effect	**Estimate**	**SE**	**z value**	**P-value**
Intercept	-0.729	0.370	-1.970	0.049
Farming system	-0.467	0.751	-0.621	0.534
Pesticide use	0.425	0.722	0.589	0.556

Table A23.11. Binomial GLMM model output for Seed count ~ Farming system + pesticide use (as a binary factor) for Bramley. Conventional pesticide use was the reference level. Theoretical marginal R^2 = 0.068, conditional R^2 = 0.068.

Fixed effect	**Estimate**	**SE**	**z value**	**P-value**
Intercept	-2.319	0.303	-7.667	<0.001
Farming system	-0.447	0.403	-1.110	0.267
Pesticide use	1.444	0.483	2.990	0.003

8.24 Appendix 24: attributes of the modelled agroforestry system (Chapter 6)

The table in this appendix sets out attributes of the theoretical modelled agroforestry system in Chapter 6, based on the agroforestry system at Whitehall Farm applied to an average-sized Cambridgeshire field.

Variable	**Value**
Field size	16 ha
Field length and width	400 m
Width of crop alley and gap at each end of tree row	24 m
Tree row width	3 m
Length of tree rows (accounting for 24 m gap at each end for machinery)	352 m
Number of tree rows	14
Total number of trees at 3 m spacing	1642
Trees per ha	102
Proportion of field occupied by tree rows	9.2 %

8.25 Appendix 25: results converted to pound sterling (Chapter 6)

This appendix sets out the findings of Chapter 6 in pound sterling currency, applying an exchange rate of £1 = €1.18.

Table A25.1. Corresponds to Table 6.3 of Chapter 6: value of pollination (£/ha/year of agroforestry) in no-spray agroforestry-grown apples, compared with orchards, using seed counts to predict apple weight, grading and fruit set. Positive values represent higher pollination value in agroforestry than orchard systems.

Apple production level	**Value of apple pollination in agroforestry compared with:**			
	Conventional		Organic	
	Bramley orchard	Braeburn orchard†	Bramley orchard*†	Braeburn orchard*†
Low	38.57	26.22	-1.53	-1.89
Average	63.39	43.10	-12.26	-15.12
High	88.20	59.98	-19.93	-24.57

* Only one site was available

† difference in seed counts between agroforestry and orchard systems was not significant

Table A25.2. Corresponds to Table 6.5 of Chapter 6: Economic performance of agroforestry (AF) compared with equivalent arable systems, under 18 different scenarios of management regime, arable crop productivity level (PL) and apple productivity level (as defined by farm management handbooks). Cumulative gross mixed income is represented by net present value (NPV), whilst EAV is the equivalent annual value for a 20-year system lifespan. All financial values (NPV/EAV) are expressed as £/ha.

Scenario			**Years for AF NPV to exceed arable NPV**	**Arable EAV**	**AF EAV with establishment costs**	**AF EAV without establishment costs**	**Carbon EAV (market price)**	**Carbon EAV (shadow price)**
Inputs	**Arable PL**	**Apple PL**						
Conventional	Low	Low	12	82.21	178.26	298.47	39.81 – 57.25	47.47 – 68.28
	Low	Average	8	82.21	402.74	522.94		
	Low	High	7	82.21	627.20	747.42		
	Average	Low	13	267.31	346.33	466.54	40.88 – 58.32	48.76 – 69.56
	Average	Average	9	267.31	570.81	691.02		
	Average	High	7	267.31	795.28	915.48		
	High	Low	14	457.49	519.03	639.23	42.00 – 59.45	50.10 – 70.90
	High	Average	9	457.49	743.49	863.70		
	High	High	7	457.49	967.96	1088.17		
Organic	Low	Low	Infinite	8.82	-231.14	-81.23	38.10 – 55.54	45.52 – 66.32
	Low	Average	11	8.82	194.99	344.91		
	Low	High	8	8.82	499.37	649.28		
	Average	Low	Infinite	98.24	-149.95	-0.03	38.48 – 55.92	45.97 – 66.77
	Average	Average	11	98.24	276.19	426.09		
	Average	High	8	98.24	580.56	730.47		
	High	Low	Infinite	229.21	-31.03	118.89	38.56 – 56.42	46.55 – 67.35
	High	Average	11	229.21	395.10	545.01		
	High	High	8	229.21	699.48	849.39		

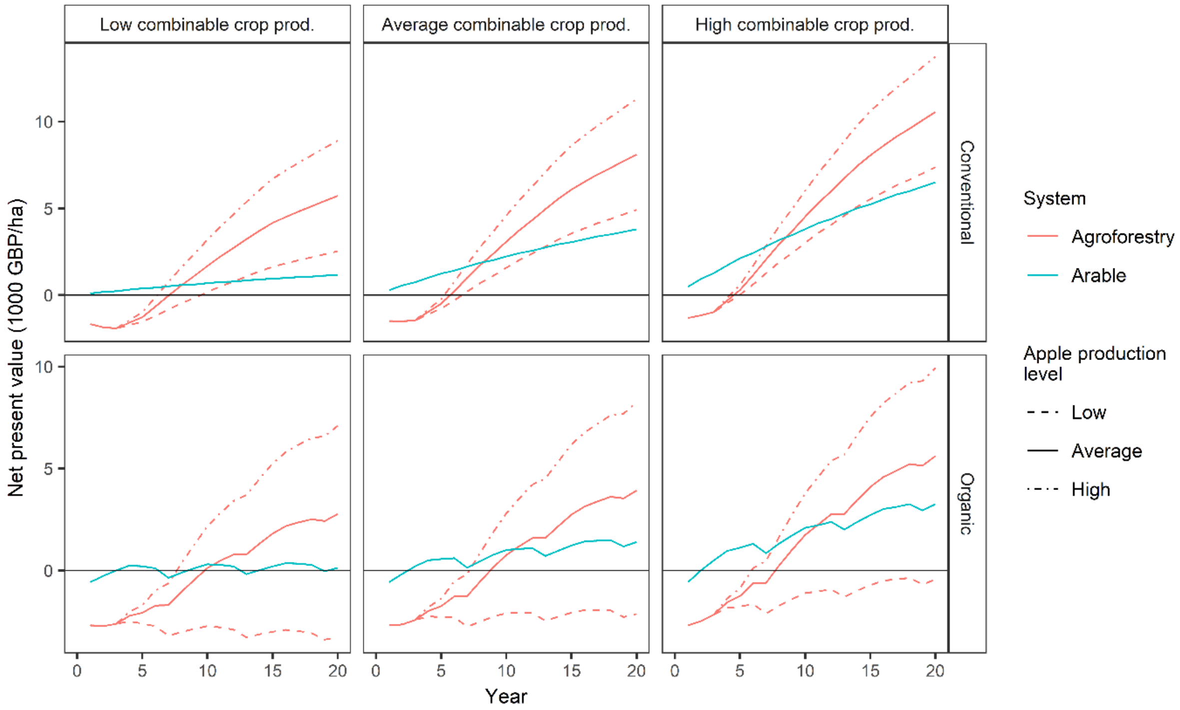


Figure A25.1. Corresponds to Figure 6.1 of Chapter 6: Modelled cumulative gross mixed income (expressed as net present value) of agroforestry versus arable systems over a 20-year system lifespan. Each column represents a combinable crop productivity level, whilst the rows represent conventional or organic management.

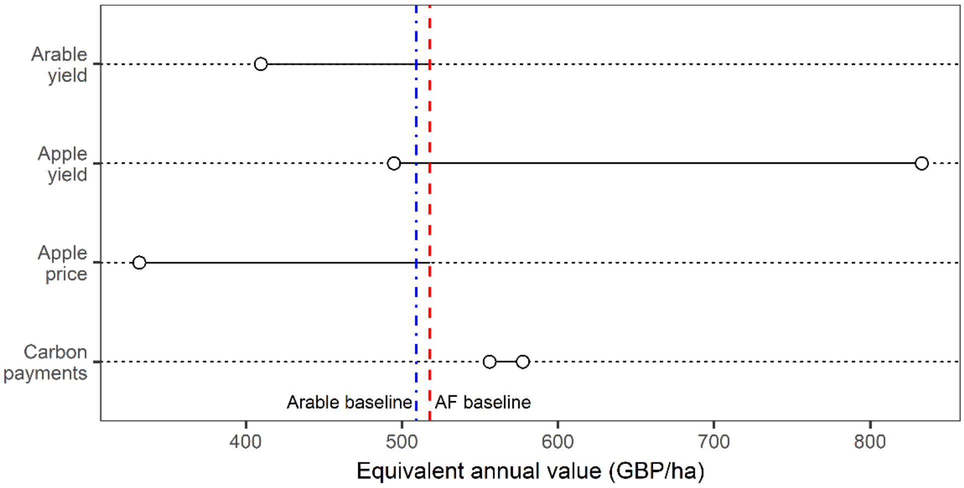


Figure A25.2. Sensitivity analysis to compare alternative scenarios for the agroforestry system. The arable and agroforestry (AF) baseline scenarios are mean equivalent annual values (EAV) from the case study simulation. The points represent mean EAV of agroforestry under the following scenarios, with inputs manipulated in isolation: the arable yield scenario assumes 11.4% reduction in arable yield in the agroforestry system (from Section 6.4.1), the apple yield scenarios represent the minimum yield recorded from the case study farm (4 t/ha, excludes establishment years) and the maximum yield from an agroforestry system (Section 6.4.2), the low apple price scenario assumes a processing price of 0.2 £/kg for all apples (compared with 70% Class 1/2 at 0.9 £/kg for the baseline scenario), and the carbon scenarios represent grant payments for carbon sequestration (Section 6.4.3).

8.26 Appendix 26: data sources for productivity scenarios (Chapter 6)

The table in this appendix sets out data sources for the productivity scenarios in Chapter 6. Arable elements refer to the arable control system, as well as the arable component of the agroforestry system. All agroforestry values were adjusted for proportion of the system occupied by trees/arable. All apple values are based on dessert rather than culinary. 'Nix' refers to Redman (2017), 'OFMH' refers to Lampkin et al. (2017).

Variable	**Conventional**	**Organic**
Arable yield (tonnes per ha of arable)	Low, average and high production levels (Nix): Winter wheat: 7.25 / 8.6 / 10 Oilseed rape: 3 / 3.5 / 4	Low, average and high production levels (OFMH): Red clover: 0 Winter wheat: 3.8 / 4.2 / 5 Winter oats: 3.5 / 4 / 4.5 Spring beans: 2 / 2.7 / 3.5 Winter triticale: 2.5 / 3 / 3.5 Spring barley: 3 / 3.2 / 3.8
Apple yield (tonnes per ha of apple trees)	Low, average and high production levels (Nix), adjusted for tree density: 14.55 / 23.91 / 33.27	Low, average and high production levels (OFMH): 2 / 16 / 26. OFMH tree density similar to agroforestry tree rows (1428/ha vs. 1109/ha), so unadjusted for density.
Apple yield reduction during establishment	Years 1-3: no yield. Years 4-5: 50% yield. Years 6-15: 100% yield. Years 15-20: 75% yield (Briggs & Knight 2019).	
Arable price (Euros per tonne)	Winter wheat: 165.20, oilseed rape: 365.80 (Nix)	Winter wheat: 277.30, winter oats: 289.10, spring beans: 354.00, winter triticale: 259.60, spring barley: 277.30 (OFMH)
Apple price (Euros per tonne)	Average of high and low values (Nix): 872.02	OFMH, based on 70% Class 1/2, 30% processing: 1062.00
Subsidies (Euros per ha)	258.15 (Basic Payment Scheme plus greening, equivalent for agroforestry and arable.)	330.75 (as conventional, plus organic land management payments under Countryside Stewardship.)

Arable variable costs (Euros per ha of arable)	Seed, fertiliser, sprays (Nix): Winter wheat: 542.80 Oilseed rape: 499.14	Seed, fertiliser, occasional costs such as casual labour (OFMH): Red clover: 204.02 Winter wheat: 205.79 Winter oats: 203.43 Spring beans: 281.31 Winter triticale: 216.41 Spring barley: 224.67
Apple harvest costs (Euros per tonne)	444.60 (harvesting, grading/packing, packaging, transport, commission/levies) (Nix)	519.40 (picking, grading/packing, storage, transport, commission, others including levies) (OFMH)
Other apple variable costs (Euros per ha of apple trees)	1732.24 (pruning/clearing, fertiliser/spray, crop sundries, based on low density orchard) (Nix)	2115.70 (pruning, crop protection, fertilisers) (OFMH)
Tree establishment costs (Euros per ha of agroforestry)	1841.10 (fencing, land preparation and drainage, trees, tree protection including stakes and guards, fertiliser, planting, irrigation; adjusted for tree density) (Nix)	2301.34 (trees, tree protection including stakes and guards, planting (all adjusted for tree density), plus drill and establish swards, irrigation) (OFMH)
Tree removal costs (Euros per ha of agroforestry)	186 €/ha of agroforestry in year 20. Calculated based on expected costs of $1000 per acre of trees (UC Davis 2019), which was adjusted to hectares, proportion of agroforestry occupied by trees (9.2%), and converted to Euro currency.	
Fixed costs (Euros per ha)	802.40 (based on 'mainly cereal farm' under 200 ha, including paid labour, casual labour, power and machinery, overheads, and rent, but excluding unpaid labour) (Nix).	

8.27 Appendix 27: case study further information (Chapter 6)

The table below sets out yield data for the case study site, obtained from the farm manager. Tonnes per ha is calculated per ha of crop type (e.g. apple yield is scaled up to equivalent yield per ha of apples, rather than per ha of agroforestry).

Total establishment costs were approximately 1150 £/ha of agroforestry (1357 €/ha), including cost of trees, support poles, ties, guarding, woven mulch mat, nectar-rich seed mix for the understorey, planting costs. Additional costs of 186 €/ha of agroforestry were included at year 20 to account for tree and stump removal. This was calculated based on expected costs of $1000 per acre of trees (UC Davis 2019), which was adjusted to hectares, proportion of agroforestry occupied by trees (9.2%), and converted to Euro currency.

Table A27.1 Yield data for the case study site provided by the farm manager.

Crop	**Year**	**Yield (t/ha)**
Apple	2016	4
	2017	5.5
	2018	5.25
	2019	4.5
Winter wheat	2009	4.8
	2010	4.9
Spring barley	2011	4.5
	2012	4.75
Spring wheat	2013	4
	2014	5
	2015	5.5
Winter oats	2016	6.2
	2017	6.25
	2018	6.4
	2019	6.3

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