Niche complementarity drives increases in pollinator functional diversity in diversified agroforestry systems

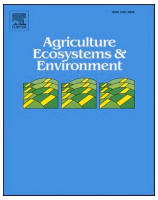
Staton, T. ORCID: https://orcid.org/0000-0003-0597-0121, Walters, R. J., Breeze, T. D. ORCID: https://orcid.org/0000-0002-8929-8354, Smith, J. and Girling, R. D. ORCID: https://orcid.org/0000-0001-8816-8075 (2022) Niche complementarity drives increases in pollinator functional diversity in diversified agroforestry systems. Agriculture Ecosystems & Environment, 336. 108035. ISSN 0167-8809 doi: 10.1016/j.agee.2022.108035 Available at https://centaur.reading.ac.uk/105208/

Agriculture, Ecosystems and Environment 336 (2022) 108035

Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

journal homepage: www.elsevier.com/locate/agee



Niche complementarity drives increases in pollinator functional diversity in diversified agroforestry systems

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ARTICLE INFO

Keywords:
Diversified farming systems
Ecological intensification
Ecosystem functioning
Ecosystem services
Functional traits
Pollination

ABSTRACT

Rising demand for food production poses a major threat to biodiversity by placing competing pressures on land. Diversified farming systems are one widely promoted nature-based solution to this challenge, which aim to integrate biodiversity-based ecosystem services into agricultural production. The underlying theory behind this approach is that diverse communities enhance ecosystem service provision, although the evidence to support this theory is often inconsistent for reasons that are not always clear. Here we investigate the contribution of pollinators to ecosystem function in a model example of a diversified farming system, silvoarable agroforestry comprising apple trees intercropped within arable fields. We assess pollinator species richness, species diversity, and functional trait diversity, between agroforestry fields and paired monoculture arable controls, and within agroforestry fields at set distances from tree rows, to quantify their potential contributions to pollination service. Species richness and diversity, and functional richness and dispersion, of wild bees were found to be significantly higher in agroforestry systems, despite weak effects on mean trait values. No significant effects were found for hoverflies. Supplemental bee species found in agroforestry systems were shown to increase functional diversity primarily by enhancing niche complementarity, effectively filling in gaps in niche space for traits, which could be partly attributed to a higher abundance and diversity of floral resources in the associated understorey. Nationally rarer bee species also contributed substantially to functional richness but not consistently to functional dispersion, suggesting that while they provide a unique functional role, their contributions to ecosystem services remain limited by low local abundances. These mechanistic insights reveal how the relationship between biodiversity and ecosystem functioning can be influenced by farm management practices through their effect on the spatial and temporal availability of habitat resources.

1. Introduction

Rising global demand for food production poses a major threat to biodiversity by intensifying competition for land (FAO, 2017). Ecological intensification and diversification aim to enhance biodiversity and harness ecological processes to improve the sustainability of agricultural production (Kremen, 2020; Simons and Weisser, 2017). By utilising synergies present in more diversified farming systems, this strategy promises to simultaneously address concerns over global food security (Mbow et al., 2019), the biodiversity crisis (IPBES, 2018; Lichtenberg et al., 2017), and resilience to predicted climate change (Gil et al., 2017; Kremen and Miles, 2012). The justification is based on the contributions of biodiversity to ecosystem services (Millennium Ecosystem Assessment, 2005), although there are often unvalidated assumptions about the extents to which additional species in a community increase the level and/or stability of the services provided. Given the current rapid decline in biodiversity (IPBES, 2019) and the emerging concept of defining an acceptable loss or 'safe limit' (Lade et al., 2020), there is an urgent need in ecological research to better understand and quantify the functional roles that species play.

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https://doi.org/10.1016/j.agee.2022.108035
Received 9 February 2022; Received in revised form 18 April 2022; Accepted 18 May 2022
Available online 30 May 2022

The approaches of ecological intensification and diversification aim to support species within agricultural landscapes by providing resources and refuges at a range of spatial and temporal scales, from seasonal intercropping, crop rotation, or the planting of flower-rich field margins, to the integration of a more permanent network of semi-natural habitat areas across a region (Kleijn et al., 2019; Kremen, 2020; Kremen et al., 2012). Such practises deliver strong benefits to biodiversity (Lichtenberg et al., 2017), and while they have potential to increase ecosystem services (Beillouin et al., 2021; Dainese et al., 2019; Tamburini et al., 2020), the effects are often small and inconsistent (Kleijn et al., 2019; Kremen and Miles, 2012; Rosa-Schleich et al., 2019). Furthermore, the extent to which additional species contribute to ecosystem services when scaled up across space and time remains largely unknown (Blüthgen and Klein, 2011; Gonzalez et al., 2020; Nicholson et al., 2020). If such practices are to be adopted it is important to identify and measure the functional role and potential benefits of those additional species harboured in more complex farming systems and landscapes (Kremen, 2020).

In ecological studies, functional trait analyses have the potential to yield important insights into the mechanisms underpinning ecosystem services by assessing the relative contributions of species to the community functional niche (Gagic et al., 2015; Wong et al., 2019), though studies on pollinators to date have tended to produce ambiguous findings (Bartomeus et al., 2018; Coutinho et al., 2018; De Palma et al., 2015; Kovács-Hostyánszki et al., 2017). There are two main reasons why, in general, enhancing biodiversity may have little impact on ecosystem function. First, species favoured in more 'natural' habitats tend to be disproportionately represented by less abundant 'rarer' species (Harrison et al., 2019). Second, the addition of species with similar traits may contribute little to functional diversity (Biggs et al., 2020). However, since there are multiple ways by which a species can contribute to the community niche, various metrics are needed to measure their potential impact. For example, functional identity measures a change in trait mean (Fig. 1, scenario 1) (Garibaldi et al., 2015), functional richness (FRic) a change in the amount of trait space filled (Fig. 1, scenarios 2 or 3), and functional evenness (FEve) the distribution of relative abundances in filled trait space (Fig. 1, scenario 4) (Villéger et al., 2008). One of the more robust measures of the community functional niche is functional dispersion (FDis) (Pakeman, 2014), which accounts for the contribution to multidimensional trait space as well as evenness in species' relative abundance (Fig. 1, scenarios 3 and 4).

In this study we investigated wild pollinator populations, which are important for the production of many crops (Garibaldi et al., 2011; Klein et al., 2006), within agroforestry and arable farming systems as a model to investigate the impacts of farming system diversification on biodiversity and ecosystem functioning. Agroforestry, defined as "the intentional integration of trees or shrubs with crop and animal production to create environmental, economic, and social benefits", is one example of a diversified farming system purported to benefit biodiversity and ecosystem function (United States Department of Agriculture, 2019). However, few studies have investigated these potential benefits in a systematic manner, and the evidence available is often ambiguous, particularly with respect to its impact on functional biodiversity (Pumariño et al., 2015; Staton et al., 2019; Torralba et al., 2016). Managed appropriately, agroforestry systems can substantially increase biodiversity (Boinot et al., 2020; Staton et al., 2021b; Udawatta et al., 2019), including wild pollinators such as bees and hoverflies (Varah et al., 2020), as well as farm income (Staton et al., 2022), although the extent to which these additional species contribute to ecosystem functioning remains largely untested. Here we compare the functional identity and functional diversity of wild pollinator communities (wild bees and hoverflies) in silvoarable agroforestry systems versus arable monoculture systems, and within the agroforestry systems at varying distances from tree rows. We determine whether the additional species harboured in the more diversified farming system contribute to ecosystem function through niche complementarity or are functionally redundant. We then extend our analysis to assess the specific contribution of nationally rarer species to the community niche and we evaluate how differences in functional diversity shaped by pollinator functional traits correspond to differences in functional traits of plants.

2. Methods

2.1. 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 minimal pesticide use. The agroforestry field was adjacent to the arable control field at two of the sites, while at the third site the two fields were separated by c. 800 m. All sites were situated in a landscape dominated by arable land, although the longest-established system was in a more intensive landscape. The sampled field sizes ranged from 3.0 to 12.0 ha.

Each of the agroforestry systems 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 (since planting) at the time of sampling. A flower mix was sown under the trees at the time of tree planting (see Supplementary Material 1 for species lists),

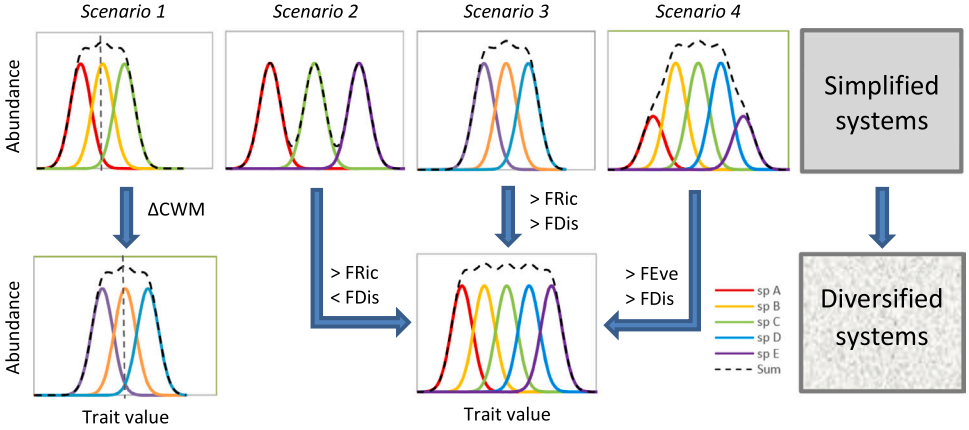

Fig. 1. Higher levels of biodiversity and ecosystem function evident in more diversified systems may be attributable to functional community changes, including functional identity represented by a directional change in community-weighted mean traits (CWM; horizontal dashed line, scenario 1), and/or niche complementarity 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.

which was cut up to twice per year during the study period as part of the standard farm management. Further information on sites, including crop rotations, is provided in Staton et al. (2021b).

2.2. Experimental design

Data were collected as part of a wider study into the impact of agroforestry systems on biodiversity (Staton et al., 2021b). 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. Wild pollinator communities were sampled using triplets of coloured pan traps over nine sampling visits across two active seasons (April to October, 2018–2019) at each of the three study sites. Pan trap samples were taken from 16 sampling points in each farming system (agroforestry and arable) at each site, spread over two alleys (including adjacent tree rows) in the agroforestry system and repeated within 'virtual alleys' in the arable controls (Supplementary Material 2 Fig. SM2.1). Pollinators were also recorded using transect walks (described in Supplementary Material 2), with the data solely used for abundance analysis (Supplementary Material 3) because specimens were identified to a broader taxonomic level (e.g. hoverfly, solitary bee, bumblebee). All sampling was undertaken at least 30 m from the nearest field boundary. Further details on the protocols for collection and identification of species can be found in Supplementary Material 2. Prior to further analyses, data were filtered and pooled as necessary to remove missing values (see Supplementary Material 2).

2.3. Analysis

2.3.1. 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 (Table 1). Bees were separated by sex/caste within the analysis, i.e. males, females, and queens were treated as separate 'species', because many species exhibit sex- and caste-specific wing length. Wing length was chosen over other size metrics such as body size or intertegular distance because sex/caste-specific data for wing length was available for all species in our dataset. Traits which were considered but not included in the analysis comprised; hoverfly proboscis length, because values depended on the method of measurement and could not be sourced for some species, and nesting placement and diet breadth of bees, because most species observed were ground-nesting and polylectic.

2.3.2. Functional identity

All analysis was undertaken using R version 3.5.3 (R Core Team, 2020). 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 within the agroforestry fields. 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 (Table 1). An additional four models were built using site as an interaction term, 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 (Table 1), with site as an environmental variable.

The count distribution (Poisson or negative binomial) and number of latent variables were selected for each model based on information criteria values and visual inspection of residual plots (e.g. to check for over-dispersion). Following this process, a Poisson distribution with two latent variables was chosen for all GLLVMs except for the hoverfly multi-trait proximity to tree row model (three latent variables). A random slope effect for farming system or proximity to tree row was included in all models, to account for species-specific variation not explained by traits (Niku et al., 2021). 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.

Table 1
Functional traits selected for the community analysis of bees and hoverflies.

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

2.3.3. Functional diversity

The 'dbFD' function in 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. 1) (Schleuter et al., 2010). These three indices are independent of each other, while the latter two are also independent of species richness (Villéger et al., 2008). Functional richness represents the volume of 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 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, and arguably provides the best estimate of niche complementarity (Mason et al., 2013). Each metric was calculated by combining all traits for the taxon (Table 1).

The effect of farming system and proximity to agroforestry tree row on functional diversity metrics was tested using log(x + 1) linear models for functional richness (because the response variable was continuous with a positive skew), binomial generalized linear models (GLMs) for functional evenness (response bounded between 0 and 1), and linear models for functional dispersion (continuous response with minimal skew). Model assumptions were checked, including for overdispersion. Separate models were built for bees and hoverflies. The functional diversity metric was the response variable, and farming system or proximity to tree row, and site, were fixed effects. In addition, because there was a significant interaction between farming system and site for bee functional dispersion, an interaction model was run with the main effect for farming system removed, to separately test the effect of farming system on bee functional diversity metrics at each site.

2.3.4. Contribution of rare bee species

We investigated the contribution of rare species to functional diversity metrics for bees but not hoverflies, because the effects of farming system on functional diversity were only significant for bees. To define rare species, an occupancy dataset was sourced (Outhwaite et al., 2019), which reports occupancy in 1 × 1 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 1 × 1 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 (Supplementary Material 4), demonstrating that our rarity categorisation was not biased by abundance in our dataset. This method of definition was preferred over Red List and Nationally Rare classifications because it is based on more recent data and allowed a reasonable proportion of species in our dataset to be classed as 'rare'.

The contribution of rare species to functional identity and each of the three functional diversity metrics (see Section 2.3.3) 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.

2.3.5. Plant floral traits

Percentage cover of plants was recorded from a 1 × 1 m quadrat at each of the pan trap sample points in June 2018 and May 2019 (Supplementary Material 2). All vascular plants observed were identified to species where possible, by the same recorder. 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 (Supplementary Material 1), 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 converted into a numeric variable according to their nectar accessibility. Functional richness and dispersion of nectar accessibility was calculated for each sample point, and the influence of farming system tested using linear models with site as a covariate. Visual inspection of trait distributions indicated distinctions between the tree rows and alley edges (0.5 m) versus alley interiors and arable fields, therefore, additional linear models were run using three treatment levels: tree row or alley edge, alley interior, and arable field.

3. Results

In accordance with previous studies, agroforestry systems yielded significantly more wild pollinators in both transects (mean ± SE: 2.71 ± 1.12 vs 1.45 ± 0.61 per transect) and pan trap samples (32.2 ± 1.24 vs 27.5 ± 1.24 per sample point), in addition to significantly higher species richness (6.24 ± 0.373 vs 4.59 ± 0.332) and Shannon diversity (1.42 ± 0.053 vs 1.18 ± 0.055) of wild bees in pan traps, compared with arable systems (Supplementary Material 3). However, there were no corresponding significant effects on species richness and diversity for hoverflies (Supplementary Material 3).

In total, 2940 specimens of 71 wild pollinator species were collected in pan traps (Supplementary Material 5), comprising 1448 specimens of hoverflies (32 species), and 1492 specimens of wild bees (39 species). A comparison between a GLLVM fourth corner multi-trait model and a null model based on these samples revealed that trait distributions between farming systems also differed for both bees and hoverflies (Fig. 2).

Trait coefficients derived from the GLLVMs revealed that bee species sampled in agroforestry systems had shorter wing lengths and longer tongue lengths than those in adjacent arable systems (CIs not overlapping zero), a finding that was consistently observed across all three sites (Fig. 2). Moreover, the size of these effects was 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. 2). Univoltinism of bees was also associated with agroforestry systems, although not consistently so among sites. Despite these clear results for bees, no corresponding patterns could explain the response of hoverflies to farming system, due to weak and inconsistent responses among sites (Fig. 2).

Repeating this modelling analysis on 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. 3). Instead, these trait distributions showed greater dispersion in agroforestry systems, evident in their measure of trait variance. Moreover, flight period was significantly longer among species recorded in agroforestry vs. arable systems, and appeared to be more dispersed (Fig. 3), despite no significant effects in the multi-trait analysis.

The apparent generality of the emerging pattern of higher trait richness and dispersion of the bee community in agroforestry versus arable systems (Fig. 3) was confirmed by an analysis of pooled bee traits, where functional richness and dispersion (but not evenness) were significantly higher in agroforestry than arable systems (richness: estimate=0.3779, t = 3.056, p-value=0.003, evenness:

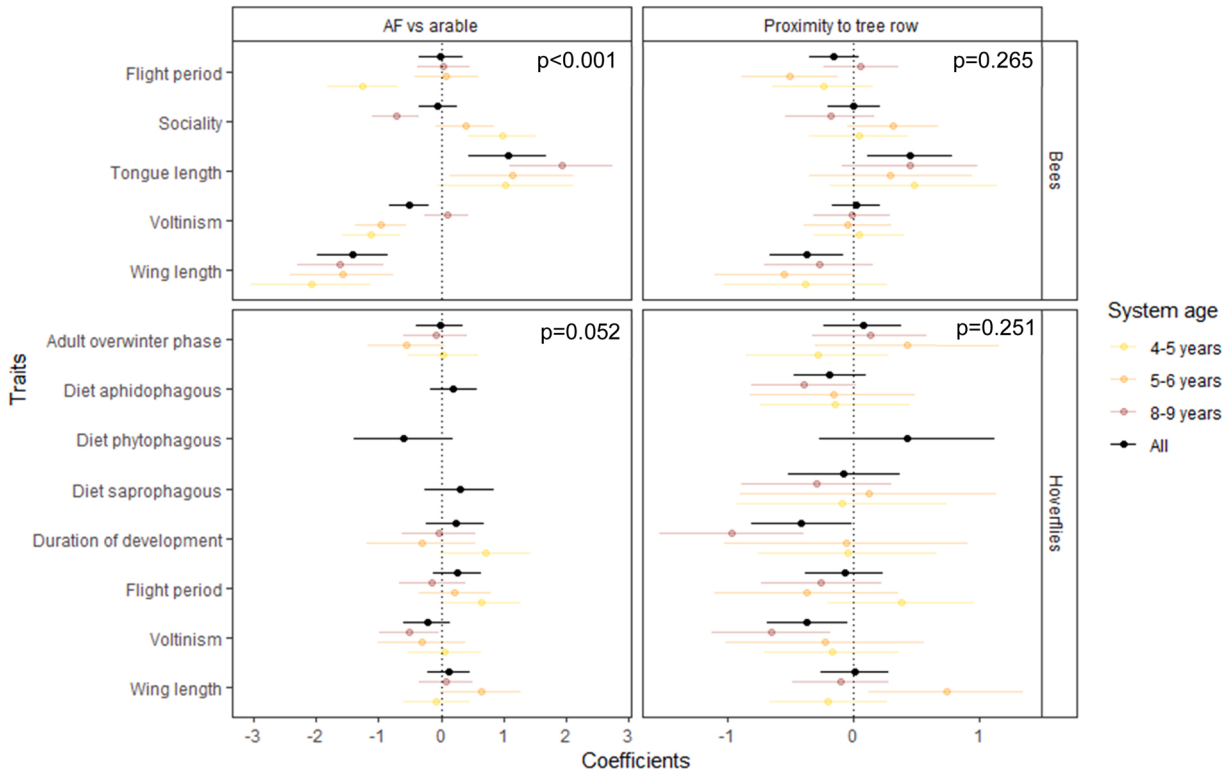

Fig. 2. Estimated coefficients (points) and 95% confidence intervals (lines) for bee and hoverfly traits, according to GLLVM fourth-corner models using pan trap data. Points with x > 0 indicate that higher trait values are associated with agroforestry (AF) rather than arable systems (left column) or 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 pooled-site fourth corner trait GLLVMs compared against null models without the trait interaction terms, where significant effects indicate 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. Some site-level outputs for hoverfly diet are not displayed due to the very wide confidence intervals (which all overlap 0), but were included in the models.

estimate=0.005, t = 0.149, p-value=0.882, dispersion: estimate=0.207, t = 2.561, p-value=0.012). However, there were no corresponding significant effects of proximity to tree row (richness: t = 0.686, p-value=0.496, evenness: t = 1.681, p-value=0.100, dispersion: t = −0.020, p-value=0.984). We found a significant interaction between farming system and site on functional dispersion, which increased with system age (although other factors may have a role as discussed below), while functional evenness followed a similar trend, but was not significant (Fig. 4). In contrast, farming system had no significant effect on hoverfly functional richness (t = 1.191, p-value=0.237), evenness (z = 0.112, p-value=0.911) or dispersion (t = 0.155, p-value=0.877).

To evaluate the additive contribution of rarer species to ecosystem function, we compared the results of analyses conducted above to repeat analyses excluding rarer species (see Section 2.3.4 for our working definition of rarity based upon national distribution). The exclusion of rarer species from single-trait GLLVMs reduced p-values for two of the five trait models (Fig. 3). Rarer 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). At the most established agroforestry system, where the effect of farming system on functional dispersion was strongest, the inclusion of rarer species decreased the significance of functional dispersion, suggesting that the abundance of common species had a more important role. However, at the second-oldest system, rarer species did contribute to the significance of functional dispersion, while at the most recently established system, rarer species had no discernible effect, suggesting that these species did not occur in sufficient abundance to influence ecosystem function at all sites.

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. Although there was no overall significant difference in floral class richness or dispersion between agroforestry versus arable systems (richness: t = 1.765, p-value=0.086, dispersion: t = 1.418, p-value=0.165), functional richness and dispersion were significantly higher in the tree rows and alley edges (0.5 m) than in arable fields (richness: t = 2.485, p-value=0.0179, dispersion: t = 3.324, p-value=0.002). 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 (Fig. 5), which are more favourable to pollinators with long and short tongues, respectively.

4. 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 bees, which has been the focus of previous studies and has led to inconsistent findings (Bartomeus et al., 2018), but also functional richness and dispersion. These findings highlight the importance of niche complementarity for ecosystem functioning, and reveal mechanistic insights into bee community differences between farming systems.

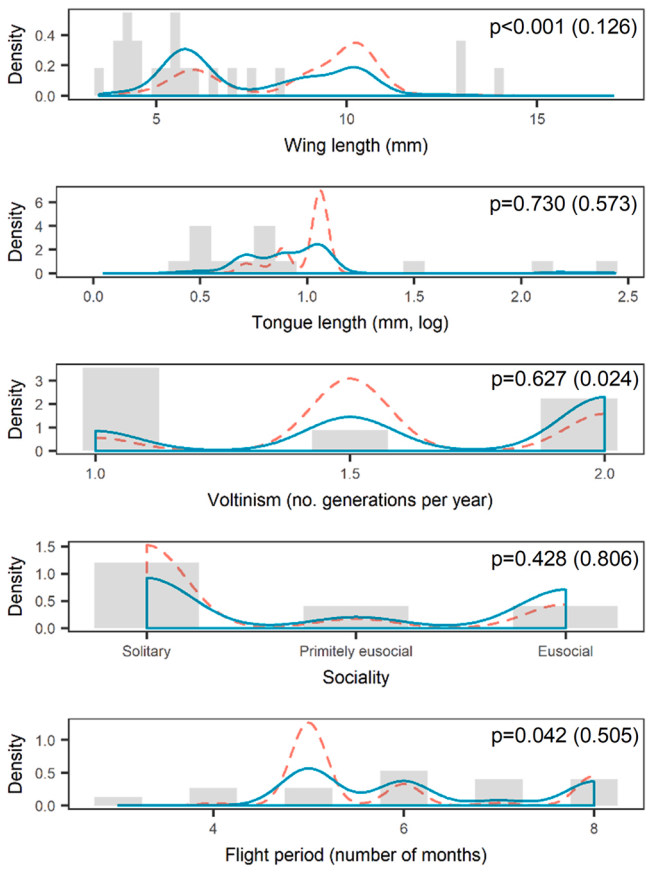

Fig. 3. Density plots (smoothed histograms) of five bee traits in arable (dashed red) and agroforestry (solid blue) systems, overlaid on density histograms showing the trait distributions of rare species (grey). For the wing length trait, species are separated into different sexes, hence there appear 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 community responses to farming system. P-values in brackets were calculated using a subset of the dataset without rare species. See Table 1 for trait definitions and coding.

4.1. Niche complementarity in bee communities

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 also identified as a significant factor when 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. 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).

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. 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. 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 have a longer flight period, at least in the single trait models. Together, the observed changes in bee trait distributions are consistent with the predicted consequences of increased availability of floral and ground-nesting resources in both space and time in the agroforestry systems.

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 and 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 (albeit only across three sites), demonstrates that these additional species were sufficiently abundant to measurably contribute to ecosystem function (Woodcock et al., 2019). 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. Regionally rare species can be locally important crop pollinators (Hutchinson et al., 2021a; MacLeod et al., 2020), although they may have a limited role at individual sites (Nicholson et al., 2020). Those species which benefit from agroforestry systems may nonetheless still have a role in contributing to regional-level ecosystem functioning (Winfree et al., 2018) and by promoting the resilience of pollination service to extreme climatic events (Kühsel and Blüthgen, 2015).

4.2. Contrasting response of hoverfly vs bee communities

Although bee species richness, species diversity, functional richness, and functional dispersion were significantly higher in agroforestry than arable systems, there were no corresponding significant effects on hoverflies, reinforcing previous reports of differences between these two taxa in respect to their responses to land use and management (Meyer et al., 2017; Persson et al., 2020; Verboven et al., 2014). This result could be attributable to a lack of strong association of the studied traits with community functional niche (Blüthgen and Klein, 2011; Kremen and M'Gonigle, 2015), a key limitation of the hypervolume approach (Blonder, 2018). However, as central place foragers, bees are known to be 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). For example, although agroforestry tree rows might be expected to provide favoured overwintering habitats for many (especially non-aphidophagous) hoverfly species (Raymond et al., 2014), the high dispersal ability of hoverflies could mask any such benefits at the scale of our study. Larval microhabitat and diet, two of the most important functional traits previously shown to determine species distribution in hoverflies (Schweiger et al., 2007), might not substantially differ between farming systems for the

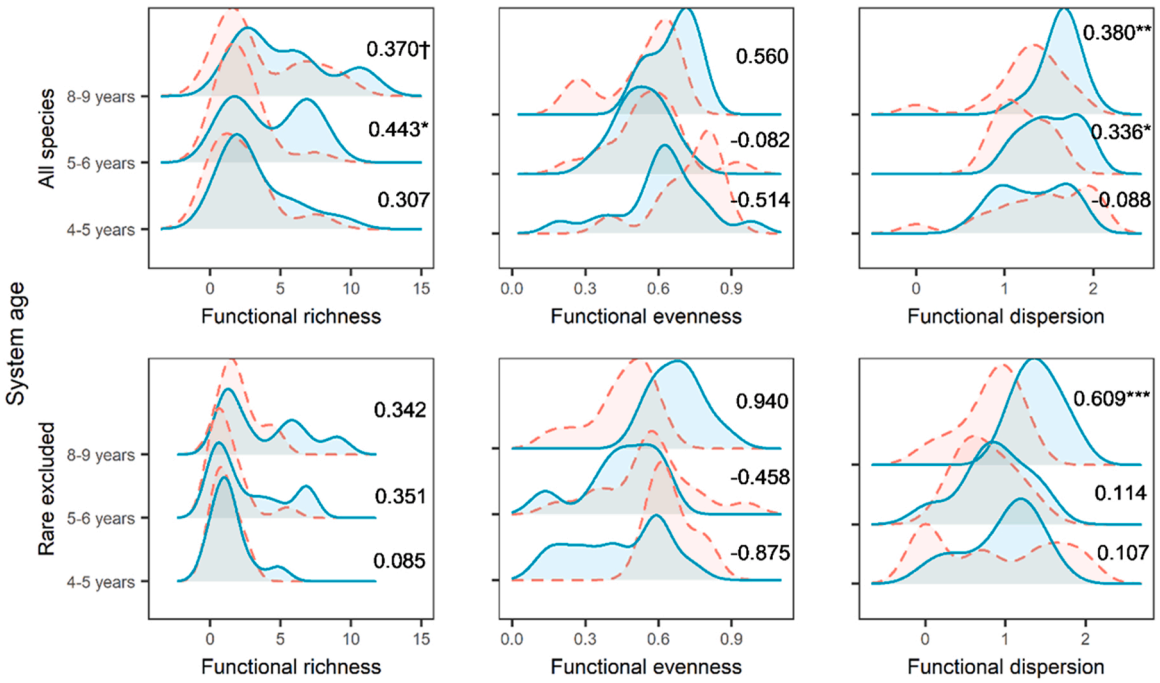

Fig. 4. Density plots showing functional richness, evenness, and dispersion in agroforestry (solid blue) and arable (dashed red) systems, calculated using all five bee traits, and separated by site. The top row represents all species, while the bottom row excludes rare species from the dataset (for both 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.

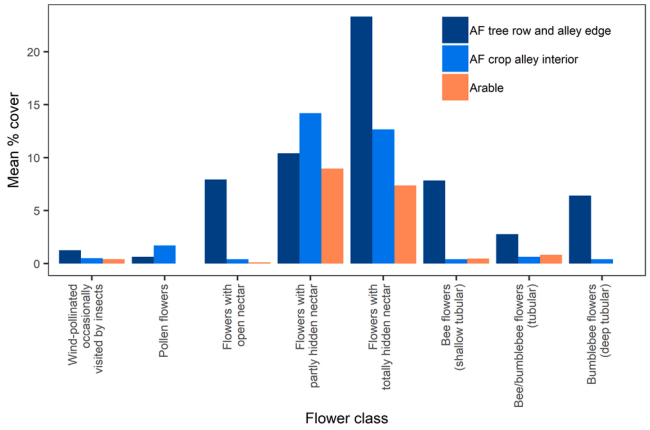

Fig. 5. Percentage cover of non-crop plants according to flower classes, ordered by nectar accessibility (decreases along x-axis), in agroforestry (AF) tree rows and alley edges (0.5 m from tree row), crop alley interiors (5 and 9.5 m from tree row), and arable systems. Wind-pollinated plants are not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

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.

4.3. Management implications

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 higher floral and nesting availability and 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., 2021a; Staton et al., 2021a). This could be achieved by establishing a flower strip under the tree rows, as was practiced at our study sites. Low intensity management to promote a diverse flowering resource can promote pollinator visitation and biological control of tree pests (Staton et al., 2021a), albeit an early-summer cut may be advisable on nutrient-rich soils (Kirmer et al., 2018). Other strategies to promote pollinators in agroforestry systems could include wider permanent vegetation strips (Cole et al., 2015), enhancement of woody vegetation diversity (Garratt et al., 2017), and creation of scraped bare ground for nesting (Nichols et al., 2020).

4.4. Caveats and research needs

Our analyses of functional trait distributions rely on data obtained from pan traps which, for some taxa such as bumblebees and hoverflies, are known to be less effective in flower-dense habitats where they may be less attractive than the surrounding flowers, and are less likely to catch large-bodied species (Hutchinson et al., 2021b; O'Connor et al., 2019; Westerberg et al., 2021). The consequences of any such sampling bias here would be to primarily underestimate our reported increases in abundance and species diversity in agroforestry systems. Differences between systems might also be underestimated by 'spillover' effects

between the agroforestry and arable fields at the spatial scale of sampling. Despite ensuring sample points were positioned well away from field boundaries (> 30 m), these fields were nonetheless adjacent at two of our three sites. However, rectification of any such biases is only expected to strengthen the statistical significance of our main findings for a significant effect of the agroforestry systems.

The results of this study are, to our knowledge, the first to reveal how additional biodiversity harboured in agroforestry systems can increase ecosystem function and services though niche complementarity, though to fully understand the generality of our findings, other agroforestry systems will need to be investigated, and in other landscape contexts (Boinot et al., 2022). For example, the increases in arthropod and pollinator species seen in croplands with agri-environmental management schemes are mostly observed in simple landscapes (Batáry et al., 2011). The Habitat Amount Hypothesis (Santos et al., 2022) attributes this to an increase in habitat complexity, which we might expect to be greater in longer established agroforestry systems. Trees can also impact habitat complexity indirectly, through their influence on soil and plant community structure and biodiversity (Tinya et al., 2021). Previous experimental trials revealed the predominant influence of understorey vegetation on arthropod diversity in agroforestry systems (Staton et al., 2021a). It should be noted, however, that the benefits of agroforestry systems to some elements of biodiversity may only be evident in organic fields or fields with minimal pesticide use, and that spillover effects into conventionally managed arable crops are likely to be much more limited (Boinot et al., 2020).

4.5. Conclusion

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, factors that can be optimised through appropriate management to promote greater sustainability. While the greatest contributions to ecosystem function come from an increase in the abundance of the more common species, rarer species still offer unique if not consistent contributions. Whatever the contribution of rarer species to ecosystem function and resilience in the face of anthropogenic change, diversified farming systems such as agroforestry can help to conserve them in the wider landscape.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

The data presented in this study are available from Mendeley Data at https://doi.org/10.17632/4fnpr4n2m5.2

Acknowledgements

The work was funded by the Natural Environmental Research Council and University of Reading (QMEE CDT, NE/R012229/1) and Formas (2019–00539). Sian K Davies (funded by University of Reading's Undergraduate Research Opportunities Programme) and Hannah J Davies contributed substantially to insect identifications. We thank the farmers of the study sites for their enthusiastic participation, Helen Chesshire (the Woodland Trust) for helping identify suitable sites, and Fiona Gierer for assisting with fieldwork. We are grateful to two reviewers for their constructive comments.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2022.108035.

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