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Temperate agroforestry systems provide greater pollination service than monoculture

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Abstract

Insect pollination is a globally important ecosystem service, contributing to crop yields, production stability and the maintenance of wild plant populations. Ironically, agriculture is one of the major global drivers of wild insect pollinator decline. At the same time, increasing human population is driving ever greater demands on crop production. Agroforestry (AF) – a more diverse farming system integrating woody and agricultural crops – can theoretically reconcile high production with provision of ecosystem services such as pollination. However, empirical studies of pollination in temperate AF systems are almost entirely lacking. We sought to fill this knowledge gap by assessing whether AF can provide increased pollination service compared to monoculture (MC) systems. Six UK sites, each containing an AF and a MC system, were studied over three years. Wild pollinator abundance and diversity were used as proxies for the magnitude and stability, respectively, of the pollinating community. We also directly measured pollination service as seed set in a wild plant phytometer. We found that temperate AF systems can provide greater pollination service than MC: AF treatments had twice as many solitary bees and hoverflies, and in arable systems 2.4 times more bumblebees, than MC treatments. AF also had 4.5 times more seed set compared to MC in one of the two years. At 40% of site-by-year sampling units, species richness of solitary bees was on average 10.5 times higher in AF treatments. This provides evidence in favour of the expectation that AF systems can support higher pollinator richness, and therefore greater potential stability, of pollination service. For the other sampling units, and for bumblebees (*Bombus* spp.), there was no treatment effect on species richness. Further work is needed to investigate the effect of AF on species richness and its mechanistic basis. Our results also highlight the importance of AF system design, ensuring that ecosystem services outcomes are explicitly planned at the design stage. We suggest that AF has a role to play in improving the sustainability of modern farming and in mitigating the ongoing loss of wild pollinating insects, which is strongly driven by prevailing agricultural practices.

Keywords: Agroforestry, pollination service, bumblebee, hoverfly, solitary bee, abundance, richness

1. Introduction

Intensive agriculture is one of the primary causes of biodiversity loss globally (Foley et al., 2005; IPBES, 2019; Newbold et al., 2015); ironically, it is also heavily reliant on biodiversity to support the ecosystem functions and services that underpin food production (Dainese et al., 2019; Garibaldi et al., 2013). Of these, pollination service has received particular attention as 35% of global crop production volume is dependent on insect pollination to some extent (Klein et al., 2007), and pollinators affect both the quantity (Castle et al., 2019; Fijen et al., 2018) and quality (Garratt et al., 2014; Klatt et al., 2013) of food produced. Despite widespread awareness of their importance, wild pollinating insect abundance and diversity continue to decline in some regions of the world (Potts et al., 2016, 2010; Powney et al., 2019). These pollinator declines, as for wider biodiversity, are driven in large part by agricultural intensification (Goulson et al., 2015; Grab et al., 2019). There is consensus that agriculture-related factors (habitat loss, and pollutants such as synthetic pesticides and fertilisers) are amongst the major drivers of insect declines worldwide (Sánchez-Bayo and Wyckhuys, 2019; Vanbergen and the IPI, 2013). These reductions in pollinator abundance and diversity are thought to have negative effects on global food production and wild plant pollination (Grab et al., 2019; Potts et al., 2016): global trends are already showing lower mean relative yields and lower yield growth in crops with greater pollination dependence (Deguines et al., 2014; Garibaldi et al., 2011a).

Efforts to mitigate loss of biodiversity in farmed land focus largely on increasing wild plant diversity as it is known that this can benefit wild pollinating insects (Isbell et al., 2017; Kovács-Hostyánszki et al., 2017). In Europe, practical interventions to increase floral resources and plant structural diversity on farmland have predominantly been encouraged through agri-environment schemes introduced via the Common Agricultural Policy. These have had some positive effects on wild bees (Scheper et al., 2013) but have less success at increasing biodiversity in field centres (Batáry et al., 2015) and, overall, numbers of insect pollinators continue to decline in many areas of the world (Goulson et al., 2015; Potts et al., 2016; Powney et al., 2019).

The trade-off with biodiversity loss has been high yields; however, it is becoming evident that the yield benefits of intensive agriculture are beginning to plateau and, in some countries, are even falling (Lin and Huybers, 2012; Ray et al., 2012). At the same time, global population and thus food demand are increasing. These facts, combined with the continuing degradation of agroecosystems and the realisation that farmed land is no longer providing the ecosystem services it once did, have led to calls for more environmentally sustainable, yet still intensive, farming practices (Garibaldi et al., 2016; Isbell et al., 2017; Pretty et al., 2018). These recognise the key role that biodiversity plays in food production (Dainese et al., 2019; IPBES, 2019; Rockström et al., 2017). Research is needed to ascertain the implications for pollinators of these alternative farming practices (Dicks et al., 2013).

AF is one such practice, integrating woody species with crop or livestock species. In modern AF systems, crops/livestock are grown in alleys between tree rows which can produce timber, fruit, nuts or any other woody product (Smith et al., 2012). It thus has inherently greater plant diversity per unit area (in terms of both crops and wild plants, such as those in the tree row understorey). Furthermore, this increased plant diversity extends throughout the field rather than being confined to field margins. Thus, in intensively-farmed landscapes, AF systems could benefit biodiversity by increasing the permeability of the agricultural matrix (Vandermeer and Perfecto, 2007). Indeed, improving habitat in the cropped area has been shown to be of greater relative importance in mitigating biodiversity loss than improving habitat in field margins (Butler et al., 2009). AF systems also increase edge density in agroecosystems, which has been shown to increase insect pollinator abundance and promote ecosystem service provision (Martin et al., 2019).

The interactions created in AF systems, when carefully managed, are theorised to provide numerous benefits (Jose, 2009; Kay et al., 2018; Kuyah et al., 2017) for example through improved provision of nesting, shelter and foraging resources (Kay et al., 2019; Nicholls and Altieri, 2013; Persson et al., 2015). Foraging resources, in particular, directly regulate bee populations (Roulston and Goodell, 2011), and bee populations also respond positively to linear elements (Kallioniemi et al., 2017). Despite its proposed benefits, AF remains understudied in temperate systems and implementation has been low; due, in part, to lack of data demonstrating the economic and environmental outcomes of these systems (Meyer, 2012; Rhodes et al., 2018; Valdivia et al., 2012). In the tropics, there is evidence of improved pollinator abundance and diversity in AF systems (Briggs et al., 2013; Hass et al., 2018; Hoehn et al., 2012) but applied work on pollination in temperate AF systems is almost non-existent: before this study (for preliminary results see Varah et al. (2013)) there was just one case study which found increased abundance of airborne arthropods in an AF system (Peng et al., 1993).

To help fill this knowledge gap, we aimed to assess whether AF can benefit wild pollinators. To do this we compared wild insect pollinator abundance, species richness, and pollination service in six paired organic AF and MC systems in the United Kingdom (UK). We focused on wild insect pollinators (we chose bumblebees (*Bombus* spp.), solitary bees, and hoverflies (Syrphidae)) because (a) the majority of pollination service is provided by wild, rather than managed, pollinating species (Breeze et al., 2011; Garibaldi et al., 2013; Smith et al., 2011), and (b) although honey bees are important crop pollinators, their abundance is primarily driven by beekeeper decision-making rather than environmental factors. We assumed that a greater abundance and/or greater diversity of pollinating insects results in improved pollination service; either in terms of the magnitude of the service, which has been linked more closely to pollinator abundance (Castle et al., 2019; Garibaldi et al., 2013; Winfree et al., 2015; Woodcock et al., 2019), or the stability of the service, linked more closely to pollinator diversity (Garibaldi et al., 2011b; Hoehn et al., 2008; Winfree et al., 2018).

We predicted:

1. Higher pollinator abundance in AF than MC.
2. Higher pollinator species richness in AF than MC.
3. Higher pollination service in AF than MC.

2. Methods

2.1 Study sites and experimental design

The effect of AF systems on pollination service was assessed in the UK using paired fields, one of which had an agricultural crop plus a tree crop (the AF treatment), the other of which had only the agricultural crop (the MC treatment). In this way we set up six sites, each with an AF system paired with an 'equivalent' agricultural MC. No suitable forestry MC (or other woody species MCs) were available, so comparison of AF *vs* tree MC systems was not possible. Sites were chosen based on several biological and logistical considerations (Appendix A). The sites encompassed a range of landscape contexts, regions and AF types (Table A.1), allowing broad conclusions to be drawn about UK AF systems. Both arable AF (silvoarable) and pasture AF (silvopasture) sites were included. A summary of fieldwork carried out at each site is given in Appendix A, Table A.2.

Paired fields were located on the same farm in order to control for landscape and site-specific effects. They were matched as closely as possible in terms of soil type, slope, aspect and previous management. The only exception was at the Suffolk site (WAF) in 2011 where a suitable MC field was not available on site, so a paired field was chosen on a farm 8 km away. This pair was only used for some of the analyses (details below). Agricultural crop type and management were as similar as possible within each pair. Such field-scale comparisons have been shown to be a reliable way of determining effects of agri-environment management options (Kleijn and van Langevelde, 2006). All sites were managed organically (no conventionally-managed sites were available). Organic farming can support higher pollinator abundance and diversity, especially at the field scale (Gabriel et al., 2013; Lichtenberg et al., 2017), although with mixed results in grassland (Scheper et al., 2013). The implication for this study is that the observed abundance and/or diversity of pollinators is likely to be higher than had non-organic fields been used, at least in arable fields. However, as both treatments were organic, the comparison remains valid and any treatment effect should also apply to conventional systems; and perhaps to an even greater degree, as larger effect sizes have been observed with increased local contrast in floral resources (Scheper et al., 2015).

In the event of unplanned differences in the cutting regime across paired fields at pasture sites, pollinator data from the affected sampling occasion(s) were excluded from analyses (Tables A.3 and A.4), because differences in cutting regime and sward structure have been shown to have a major short-term effect on pollinator abundance and diversity (Buri et al., 2014; Potts et al., 2009). All data from the Suffolk site (WAF) in 2011 were excluded from bumblebee and hoverfly analyses (although retained in solitary bee analyses) because the sown ley mixtures in the paired fields differed greatly in clover abundance (it was greater in the MC treatment; further details and justifications in Appendix A). The potential impacts of these decisions were assessed in separate analyses, which gave consistent results (Appendix B, Tables B.4-B.6 & B.10) although with slightly weaker data-based model selection, indicating the decisions were justified.

2.2 Estimating pollination service

We monitored bumblebees, solitary bees and hoverflies as these are known to be the main insect pollinating taxa in the UK; butterflies contribute relatively little to crop pollination in northern Europe (Jennersten, 1984). Abundance (Section 2.2.1) and species richness (Section 2.2.2) of pollinators were used as proxies for pollination service (see Introduction for literature supporting the assumptions made here) as both have been directly linked to plant reproductive success and pollination service provision (Dainese et al., 2019; Winfree et al., 2018, 2015). Pollinator abundance was estimated using timed transect walks and species richness using pan traps (O’Connor et al., 2019). Pollination service was also measured directly using phytometer plants (Section 2.2.3).

2.2.1 Abundance

Abundance within each taxon was measured as total numbers of individuals per field recorded during a field season. Standardised transect walks were used to assess numbers of individuals. Transect walks give a good indication of habitat associations as they are area-based rather than activity-based. At each site a 200m-long transect was set up in each treatment in the spring of 2011. Unambiguously identifiable individuals seen within 2.5m on each side of the line and 2.5m in front of the observer were recorded. Because many pollinator species are hard to identify outside a laboratory setting, unidentifiable pollinator specimens were netted and killed quickly with ethyl acetate for laboratory identification. Transects were set up at least 25m from the end of the AF alley, or from the field boundary in the MC, to avoid edge effects. In AF systems, half of each transect (100m) was situated in the centre of the alley and the other half ran along the edge of the alley in order to sample both environments. Transects were walked at a rate of 5m min^{-1} between 10:45h and 15:45h, and only when weather conformed to UK Butterfly Monitoring Scheme standards (http://www.ukbms.org/Methods.aspx) as insect pollinators forage in these conditions. Weather conditions were monitored throughout the transect using a Kestrel 3500 hand-held weather meter. Transects were carried out from the end of March until the end of September in 2011 and from April-September in 2012 to encompass peak flower blooming and pollinator flight periods. At one site (WAF, site details in Appendix A) an additional survey round was undertaken in March 2013 to capture the flowering period of the tree species at that site.

One transect was walked in each treatment (AF or MC) per visit. Sites were visited between four and six times during the season (number of successful visits depended on the weather and the farm management). At most sites, five visits were achieved in 2011 and four in 2012. Visits were at least a month apart to avoid re-sampling the same individuals on each visit. Although different sites were not sampled with equal intensity, each pair of fields within a site was sampled equally. Site was included in models as a random effect, allowing direct comparisons of abundance to be made.

2.2.2 Species richness

Species richness was chosen as a suitable diversity measure because (a) it is often used in studies looking at the effects of agri-environmental management or habitat quality on pollinators (e.g. Kleijn and van Langevelde 2006, Concepción *et al.* 2012); (b) it is suitable for all spatial scales; and (c) it is an easily-understood index of community structure (Gotelli and Colwell, 2011). EstimateS was used for species richness calculations (Colwell, 2013). Sites were not all sampled an equal number of times, so rarefaction (bumblebees) and extrapolation (solitary bees) were used in order to allow analysis of species richness across all sites (Gotelli and Colwell, 2001; Colwell *et al.*, 2012). Bumblebee data was rarefied to the lowest number of sampling occasions at any site (*n*=4) as numbers caught were not high enough to allow reliable extrapolation. Solitary bee numbers were higher so species richness could reliably be extrapolated to the highest number of sampling occasions at any site (*n*=14) (an analysis of rarefied solitary bee data gave consistent results, Table B.9, Figure B.1). Workers of *Bombus terrestris* and *B. lucorum* (buff-tailed and white-tailed bumblebees) are difficult to tell apart so these two species were recorded as one aggregate species. All solitary bees were identified to species by Ellen Moss (University of Reading). Hoverfly species richness was not investigated.

Pan traps have been shown to be the best single method for assessing bee SR (Westphal *et al.*, 2008; Nielsen *et al.*, 2011). UV-bright pan traps were set up on each visit and left out from 08:00h-17:00h. Three colours (one yellow, one blue and one white pan) were used at each sampling location as different pollinator groups may be attracted to different colours (Campbell and Hanula, 2007). Sampling locations were positioned in a diagonal line across an AF alley. Six sampling locations were used per treatment in 2011, and twelve sampling locations were used per treatment in 2012 (six sampling locations in each of 2 alleys). This pattern and orientation were mimicked in the MC control fields. Pan trap sampling was carried out on the same sampling occasions as transect walks.

At arable sites pan traps were positioned on stands at crop height. At pasture sites pans were placed on the ground on a square of black mulch fabric to ensure the same background colour at each position. Insects collected from each pan were bagged and taken back to the laboratory where they were frozen until identification.

2.2.3 Seed production

In 2012 and 2013, phytometers (potted plants) were used to estimate pollination service directly at a subset of sites (Table A.2) as they are a reliable method for measuring pollination service

(Woodcock et al., 2014). The plants chosen were California poppy (*Eschscholtzia californica*) as they are self-incompatible, pollinated by generalist species, do not occur in the landscape (therefore all pollen comes from the phytometers), and the seeds are easy to count. The phytometers used in this study performed well in field trials and plants from the same batch were used successfully in other studies (Hardman et al., 2016). Hardman et. al. (2016) give further justifications for choosing California poppy.

Prior to exposure, five developing buds were tagged and all other buds removed. Plants were then placed in the field: on the ground in pasture systems and on upturned buckets in arable systems to ensure the flowers were level with the top of the crop. Phytometers were protected with chicken wire cages and 10 organic slug pellets per pot. They were watered as necessary.

Phytometers were exposed for two weeks in July and August, and additional flowers were tagged as they opened (up to 20 additional flowers in 2012, and 30 in 2013). Phytometers were then placed in pollinator exclusion cages while tagged fruits ripened (any subsequent developing buds were removed daily, and plants were watered as necessary). Seed set was assessed by counting the number of fully-developed seeds per fruit.

Phytometer positioning in the field followed the same pattern as the pan trap positions, but phytometer plants were positioned 5m further down the alley so that they were not in the same place as the pan traps. In 2012, two arable and one pasture site were used and one phytometer plant was placed at each position. In 2013 the phytometer experiment was beset with issues. First, land use could not be kept the same as in 2012 because one of the arable sites changed the crop from arable to ley and although another arable site was set up with phytometers in 2013, work there had to be abandoned due to a severe weed problem. Thus, in 2013 three pasture sites were used. Furthermore, in 2013 two plants were used per position at two of the three pasture sites but, due to unforeseen circumstances, only one plant was used per position at the third pasture site and at the (subsequently abandoned) arable site. Finally, due to an error, phytometer plants at two of the three sites (SD & WAF) in 2013 were closer to each other in MC treatments than in AF treatments. In the third site (LHF) distances were equal. The implications of these issues are discussed later. For transparency, we include an analysis of the 2013 phytometer data and attempt to account for these discrepancies; however, the results merely serve to highlight the problems inherent in the dataset. Partly because of these discrepancies, phytometer data were analysed separately for 2012 and 2013.

2.3 Estimation of other variables expected to influence abundance or species richness

Because it was not possible to control for effects other than treatment, several other possible predictors of pollinator and plant species richness and abundance were measured, based on the literature (Table A.5). These were: the species richness of insect-pollinated plants in field boundaries (both hedges and margins, method in Appendix A); the area covered by the field boundaries (measured from farm maps and Google Earth); the distance to the nearest field boundary from the data collection area (measured on the ground); the number of hedged field boundaries; the type of land use (arable or pasture); the percentage of the transect that was sunny (time estimated during transect); and the percentage of semi-natural habitat (SNH) in the surrounding landscape. %SNH in a 1km buffer around field perimeters was calculated from Priority Habitat Inventory for South East England using ArcMap 10 GIS software. This buffer size encompasses the predominant flight ranges of wild bees (Greenleaf et al., 2007; Zurbuchen et al., 2010). Further methodological details given in Appendix A.

Finally, because the effect of treatment on pollinator species richness and abundance may be mediated through treatment effects on plant species richness (Borer et al., 2012; Scherber et al., 2010), we estimated the plant species richness of the cropped area (method in Appendix A) and tested for correlations with pollinator abundance or species richness. In AF systems, the cropped area included the tree rows.

2.4 Statistical analyses

An information theoretic (IT) approach was adopted, using model averaging to allow inferences to be drawn from weighted support over several models (multi-model inference). Standard IT practice is to first generate a highly-parameterised global model with all the biologically relevant parameters (Burnham and Anderson, 2002; Grueber et al., 2011; Harrison et al., 2018). The global model (which is not used for inference) is used to generate all possible lower-dimensional sub-models (in effect, all possible hypotheses). These more parsimonious lower-dimensional models are then compared against each other to find out their relative worth. The ones with the highest relative worth are used for inference. Statistical analyses were carried out in R (R Development Core Team, 2019).

An extensive literature search was carried out to identify possible predictor variables for inclusion in global models (Table A.5) (Burnham et al., 2011; Elliott and Brook, 2007). The final choice of predictor variables and interactions included in global models was based on evidence from the literature and on basic data exploration. Variables that did not appear to be having a strong effect when investigated graphically were nonetheless included in global models if there was a scientific reason to suspect they might have some effect.

Global models (Table A.6) were all initially built as generalised linear mixed effects models (GLMMs), fitted by maximum likelihood. Model fit was based on the global model only (Burnham et al., 2011; Harrison et al., 2018; Symonds and Moussalli, 2011). To allow comparison of the relative strength of parameter estimates after model averaging, continuous independent variables were standardised prior to model building using the *arm* package (Gelman et al., 2013) or, for negative binomial models, the *rescale* function in R. For species richness and phytometer 2012 data, error structures were Poisson or Gaussian (*glmer* and *lmer* functions respectively, package *lme4* (Bates et al., 2015)). To reduce overdispersion, error structures for abundance models were Poisson-lognormal, in which observation-level random effects are used, or negative binomial (*glmer.nb* function in package *lme4*). Nested random effects were included in global models where possible because of the hierarchical nature of the study design. Where random effects explained none of the variance, they were removed from models; this resulted in single random effects (rather than nested) in some models (Table A.6). Model assumptions were verified by using standard model check plots to assess the residuals for temporal and spatial dependency. Where necessary, square root or log transformations of the response variable were used in linear mixed models (LMMs) fitted by maximum likelihood. Model validation of all global models indicated no problems (except in the phytometer 2013 global model which was not used, as explained below).

Global models were then used to generate all possible lower-dimensional models using the *MuMIn* package (Bartoń, 2019). A subset of plausible 'top' models that explained the data best was chosen from these candidate models using cut-off criteria for difference in AIC_c (Δ_i) of 4 or less, always ensuring that *S* (the number of models in the top models set) was less than the number of sites used in the analysis (maximum n = 6) (Burnham et al., 2011; Grueber et al., 2011). AIC_c was used due to the small sample size. The 'top models' subset was then used for multi-model inference. This model-averaging approach allowed us to explicitly incorporate the model selection uncertainty that can result from small datasets, resulting in robust parameter estimates with reduced uncertainty and bias (Burnham and Anderson, 2002; Grueber et al., 2011). Model-averaged parameters were calculated using the natural average method (Burnham and Anderson, 2002).

It was necessary to use a negative binomial error structure for the hoverfly abundance dataset; these models were not accepted by the *MuMIn* package, so candidate model sets were generated by hand and then models were compared using package *AICcmodavg* (Mazerolle, 2019). Model averaged parameters were then calculated from the top model set by hand (Equations A.1 – A.3, Appendix A).

We would ideally have analysed the phytometer data from both years together, but the proposed global model suffered from multicollinearity. This was due to the 2013 dataset, so we analysed the two years separately (there were no correlation issues in the 2012 data). The proposed global model for 2013 phytometer data (P-2013, Table A.6) was unusable due to multicollinearity (Table B.12), and other variations of the model suffered from the same problem. These issues persisted when we attempted to analyse each site separately. We could not, therefore, reliably use a linear model for this analysis (Freckleton, 2011). Instead we carried out a Principal Components Analysis (PCA) using the prcomp function in R core package ‘stats’. The variables included in the PCA were those originally identified as important when building the proposed global model. PCA is often used to reduce the potential number of model parameters by selecting informative variables (King and Jackson, 1999), but this was not possible here (see results).

When interpreting model-averaged results, the relative variable importance (w_{ip}) indicates the strength of evidence for each variable. The larger the w_{ip} is, the more important that variable is relative to the other predictor variables, and the more confidence we can have that it is a strong predictor of the observed response. Predictor variables are considered important if $w_{ip} > 0.6$ and if the confidence intervals do not overlap with zero (Burnham and Anderson, 2002). Unless stated otherwise, model estimates are given at the mean of all other predictor variables.

3. Results

3.1 Pollinator abundance

3.1.1 Bumblebee abundance

Pollinator abundance on transect walks was higher in AF than MC treatments (Figure 1a). A total of 1,979 bumblebees were recorded on transect walks. After eliminating sampling occasions where pasture sward structure or composition were incomparable (Appendix A), there were 1,159 bumblebees in total, of which 835 were recorded in the AF and 324 in the MC. The top models subset and results of model averaging show that the variables with the largest effect on bumblebee abundance are treatment, land use, and the interaction between these two (all have $w_{ip} = 1$ and CIs do not include zero, Tables 1 & B.1). Of these three, the variable with the narrowest CI is treatment. There is therefore strong evidence that treatment is an important (or even the most important) predictor of bumblebee abundance. Model estimated bumblebee abundance on any given transect was 1.8 in AF and 1.5 in MC. There is also very good evidence that the interaction between treatment and land use is important: model estimated bumblebee abundance was 7.6 times greater in silvoarable systems than in silvopasture systems (Figure 1a), and indeed model estimates of bumblebee abundance showed no difference between treatments in the pasture systems. In arable systems, model estimated bumblebee abundance was 2.4 times greater in AF than MC (abundance per transect = 7.0 and 2.9 respectively). Bumblebee abundance was also affected by the amount of sunshine during transects and distance to the nearest boundary hedgerow, with fewer bumblebees observed further from boundary hedgerows (Table 1).

3.1.2 Solitary bee abundance

A total of 136 solitary bees were recorded on transects, of which 133 were seen in the AF treatments and 7 in MC. Solitary bee abundance was higher in AF treatments than MC treatments (w_{ip} treatment = 1, CIs do not include zero, Figure 1b, Tables 1 & B.2). Model estimated abundance of solitary bees on any given transect was 1.4 in AF and 0.7 in MC. In addition, solitary bee numbers were lower further from hedgerows and were affected by the amount of SNH in the landscape (Tables 1 & B.2). As the amount of SNH in the surrounding landscape increased, numbers of solitary bees in AF treatments were unaffected but numbers in MC treatments increased: an increase in SNH from the mean of 11% to 35% resulted in more than a three-fold increase in numbers of solitary bees in MC systems (from an average of 0.7 to 2.3 individuals on any given transect).

3.1.3 Hoverfly abundance

A total of 1,793 hoverflies were recorded on transects (after elimination of all data collected in 2011 from site WAF, see Methods). Of these, 1,332 individuals were recorded in AF and 461 in MC. Hoverfly abundance was almost two times higher in AF than MC treatments (w_{ip} treatment = 1, CIs do not include zero, Tables 1 & B.3, Figure 1c & d): model estimated abundance of hoverflies on any given transect was 5.5 in AF and 2.8 in MC. Land use was also an important predictor (w_{ip} land use = 1, CIs do not include zero, Tables 1 & B.3, Figure 1c & d): model estimated hoverfly abundance on any given transect was three times higher in arable than in pasture land (8.3 and 2.7 respectively). Treatment had a slightly narrower CI than land use; there is therefore strong evidence that treatment was an important (or even the most important) predictor of hoverfly abundance. There is also weak evidence of an interaction between treatment and land use (Table 1): the AF treatment increased hoverfly abundance 2.9-fold in arable systems but only 1.6-fold in pasture systems. Although there is weak evidence of an interaction effect, we plot hoverfly abundance in arable and pasture land separately in Figure 1 because the far higher abundance in arable land made an interaction plot hard to read. There is weak evidence that larger boundary areas positively affected hoverfly abundance (Table 1). Date^2 also affected hoverfly abundance: this is a known seasonal effect and the variable was included to improve model fit.

3.2 Pollinator species richness (SR)

In total, 178 bumblebee individuals from 11 species were caught in pan traps (after excluding data from WAF 2011 and counting *Bombus terrestris* and *B. lucorum* as one aggregate species). All 11 species were found in AF treatments, and seven of these species were found in MC treatments. For solitary bees, a total of 1,249 individuals were caught. After eliminating from the dataset all unsuitable sampling occasions, then removing specimens in too poor a condition to identify (*n* = 6), there were 1,133 solitary bee individuals comprising 57 solitary bee species from 11 genera. 50 species were recorded in AF and 36 species in MC. There is no evidence of a treatment effect on either bumblebee or solitary bee SR: for both taxa, there is almost no difference between the best-ranked model and the null model (Tables B.7 & B.8), indicating that they are almost equally as likely as each other. Furthermore, treatment is not in any of the top bumblebee models (Tables 2 & B.7). For both bumblebee and solitary bee SR, the predictor variables present in the top models subsets either have CIs which include zero or/and they have very low w_{ip} (Table 2). Solitary bee SR results were obtained by extrapolating solitary bee data to *n*=14 sampling occasions; rarefaction to *n*=4 gave very similar results (Appendix B, Table B.9 & Figure B.1).

For both bumblebee and solitary bee SR the low Akaike weights of all the top models (Tables B.7 & B.8) indicate high model-selection uncertainty, reducing our confidence in the data-based choice of best models and reinforcing the need for multi-model inference (Burnham and Anderson, 2002). In future, more data may enable identification of a 'best' model and/or stronger inference. Although the data are not adequate to draw strong inference from the all-sites model, initial visualisation of solitary bee SR data (although not bumblebee data) suggested a difference between treatments at some sites. We therefore compared SR estimates at each site separately. This site-by-site analysis (Figure 2) showed that extrapolated SR was significantly higher in the AF treatment at sites CE in 2011, at WH in 2011 and 2012, and at WAF in 2012 and 2013 (on average it was 10.5 times higher in AF treatments). At WAF in 2011, LHF and SD the AF treatments had higher SR but not significantly so. At one site (RR) the MC treatment had higher SR, although not significantly so (Figure 2).

3.3 Relationship between plant SR and higher trophic levels

The effect of treatment on pollinator SR and abundance may be mediated through treatment effects on plant SR. To investigate this relationship, we tested Pearson's product moment correlation between plant SR and pollinator metrics. We found that plant SR and solitary bee SR were positively correlated ($r_{(8)}$=0.67, p=0.04). No other pollinator metrics were correlated with plant SR.

3.4 Seed production

Seed set in 2012 was higher in the AF treatment than in the MC treatment (w_{ip} treatment = 1, CIs do not include zero, Tables 3 & B.11). From 36 plants (on each of which up to 20 buds were allowed to develop), 335 seeds were produced. Of these, 239 seeds came from the AF treatment and 96 from the MC. Model estimated seed set was 0.9 seeds per fruit in AF and 0.2 in MC. Distance to the nearest hedgerow affected seed set, with fewer seeds produced in phytometers further from hedgerows. In AF treatments, for example, model estimated seed set 100m from the nearest hedge was 0.6 seeds per fruit whereas at 20m it was 2.2 seeds per fruit.

In 2013 seed set was much higher per plant than in 2012: from 120 plants a total of 1,703 fruits were produced, containing 58,297 seeds. Of these, 23,006 seeds were produced in the AF treatment and 35,291 in MC. Mean number of seeds per fruit was 28 in AF and 39 in MC. We investigated the relative effect of variables in the dataset using the first two principal components from the PCA as they had eigenvalues greater than 1 and together explained 72.4% of the variance (Figure 3, Table B.13). The three most representative variables on PCs 1 and 2 were the distance between phytometers, followed by treatment and boundary area in joint second place (Figure B.3).

Figure 3 shows that different variables were important at different sites. At site WAF most of the variance was on PC1. Distance between phytometers was the variable most significantly associated ($p < 0.001$) with PC1. It had a correlation of 0.98, was the largest contributor to this component (43%) and had the highest quality of representation (cos2 = 0.96) (Figure B.2, Table B.14). At WAF, the phytometers were 2.5 times further apart in the AF treatment than in the MC treatment, and the results indicate that this variable had a strong influence here. Treatment and hedge distance were also significantly associated with PC1 (both $p < 0.001$) and were joint second in terms of both contribution (each 24%) and quality (each cos2 = 0.54, Figure B.2, Table B.14): at WAF the hedges in the AF were over twice as far from the phytometers as they were in MC. Figure 3 indicates that the species richness of insect-pollinated plants in field boundaries was also a small contributor at WAF (Figures B.2 & B.3), where it was higher in the MC treatment.

At the other two sites (LHF and SD), most of the variance was on PC2 (Figure 3). This component is dominated by boundary area: its contribution and quality of representation were almost three times greater than the next most important variable on PC2, which was treatment (Figures B.2 and B.3, Table B.14). Both LHF and SD had large differences in the boundary areas of the two treatments: at LHF the boundary area of the AF field was almost 3.5 times greater than in the MC; at SD the boundary area of the AF field was 12.5 times smaller than in the MC.

Although PCA can be used to reduce the potential number of model parameters, a regression analysis using the variables that contributed most to PCs 1 and 2 would be uninformative because they are all correlated with each other (Table B.12). The PCA results indicate that other variables were more important than treatment on both PCs, so we can draw no firm conclusions about the effect of treatment on seed set in the phytometer 2013 dataset.

3.5 Summary of results

Without exception, in all multi-model inference analyses where there was evidence that one or more variable(s) affected the response, treatment was the variable with the strongest evidence of an effect. Therefore, presented below (Table 4) is a summary of treatment effects. The size and direction of the effect is shown. Excluded from this summary are those analyses where there was no strength of evidence for any variable affecting pollinators or pollination. We also exclude the phytometer 2013 data.

Table 4 shows that overall, AF treatments had a positive effect on pollinators and pollination. We highlight below some of the nuances in these results:

(i) Solitary bee and hoverfly abundance were higher in AF treatments, regardless of land use, whereas bumblebee abundance was higher in AF treatments in arable systems only; in pasture systems bumblebees showed no evidence of a treatment effect.

(ii) For bumblebees and hoverflies, the positive response to AF treatments was greater in arable land than pastureland, although for hoverflies the evidence for this interaction was only weak.

(iii) SR differences were harder to detect than abundance differences, and differences were only observed at some sites.

(iv) Only solitary bees showed a SR response to treatment; bumblebee SR showed no response.

(v) Plant SR was positively correlated with solitary bee SR, although not with any other pollinator metrics.

4. Discussion

4.1 Pollinator abundance

The higher abundance of all three wild pollinator taxa (bumblebees, solitary bees and hoverflies) in AF compared to MC treatments is compelling evidence that modern AF systems in temperate climates can support higher numbers of pollinators and thus potentially greater pollination service than MC systems. This is supported by the 2012 phytometer results where we observed a pronounced treatment effect, with 4.5 times higher seed set in AF than MC. This confirms that the higher pollinator abundance in AF treatments in 2012 was being translated into increased pollination service in these systems.

Our findings are consistent with the literature, a large body of which shows that insect abundance displays strong local-scale responses to increased plant diversity (Lichtenberg et al., 2017). The observed increase in pollinator abundance is likely to be because the AF treatments, particularly the un-grazed ones, provided more floral, nesting and larval resources, more undisturbed areas, and a more diverse sward structure. For solitary bees in particular, local-scale habitat characteristics have been shown to have a strong influence on abundance (Hopfenmüller et al., 2014; Scheper et al., 2015) and this group showed a very strong positive response to both the AF treatment and proximity to hedgerows, which can be a good resource for wild bees (Garratt et al., 2017; Ponisio et al., 2019).

We also found landscape-scale effects on solitary bees: in MC treatments, a higher percentage of SNH in the surrounding landscape was related to higher solitary bee abundance, as observed elsewhere (Bukovinszky et al., 2017; Nicholson et al., 2017). The fact that this effect only occurred in MC treatments suggests that, for solitary bees, the influence of landscape-scale factors was outweighed by local-scale factors (*i.e.* the AF treatment), in agreement with other studies (Benjamin et al., 2014; Hopfenmüller et al., 2014). AF systems thus show great potential for supporting and conserving solitary bees in UK farmland as well as providing greater levels of pollination service.

Hoverfly abundance also exhibited a strong positive response to the AF treatment, in line with findings that vegetation-structural traits and floral resource provision are important predictors of hoverfly abundance (Bartual et al., 2019; Haenke et al., 2009). Pollination service provision by hoverflies should therefore be higher in AF systems than in MC. Hoverfly abundance in both treatments was higher in arable than pasture land, which is likely to be because many hoverflies have aphidophagous larval stages so their abundance will be higher in land use types harbouring aphid populations (Haenke et al., 2009). These findings thus suggest the potential for greater natural pest control in AF systems, which has been observed in some AF systems elsewhere (Pumariño et al., 2015; Staton et al., 2019); further work would be necessary to confirm this.

Both bumblebees and hoverflies showed a greater response to treatment in arable than pasture land, in agreement with other studies which have observed greater effect sizes in arable (*i.e.* more simplified) landscapes (Carvell et al., 2011; Haenke et al., 2009; Scheper et al., 2015). In our study, the larger treatment effect in arable systems is likely to be due to the higher ecological contrast created at these sites (Marja et al., 2019): most of the pasture systems were grazed, thus removing understorey resources, whereas at arable sites the tree understoreys provided floral and nesting resources and overwintering habitat, which promote pollinating insect abundance (Häussler et al., 2017; Ramsden et al., 2015; Scheper et al., 2015). Incorporating fruit or nut trees into grazed silvopasture systems could better support insect pollinator populations through increased floral resources during the tree blossoming period (Häussler et al., 2017; Potts et al., 2009). Furthermore, our pasture sites were grazed by sheep which crop the vegetation closely and create a homogenous sward, reducing resources for pollinating insects. Other livestock, however, graze differently and so there may be potentially greater resources for pollinating insects in other livestock systems (Vanbergen et al., 2014, 2006). These factors highlight the need for careful design of AF systems, ensuring that ecosystem service outcomes are explicitly planned right from the design stage rather than being considered a coincidental bonus. Payments for Ecosystem Services schemes could help focus attention on service provision at the planning stage, and this study provides the type of quantitative evidence – linking land management to ecosystem service provision – that is required when designing these schemes (DEFRA, 2014).

Pollinator activity was not recorded, so it is impossible to know whether the observed treatment effect was having a population-level effect or simply attracting pollinators from elsewhere. It is, however, possible that the increased pollinator abundance in AF systems may be at least partly due to population-level effects as AF systems can provide many of the nesting and larval development requirements of pollinators. Nevertheless, we can say with a high degree of confidence that the higher pollinator abundance observed in AF treatments means that AF systems are a useful resource for pollinators and can therefore support pollinator populations in the wider countryside.

4.2 Pollinator species richness

In contrast to pollinator abundance, pollinator SR did not exhibit such a pronounced treatment effect (as also observed elsewhere, e.g. Bukovinszky et al. (2017)). Our confidence in the results of the all-sites analyses was low and the results indicated a need for more data: it is thus likely that we did not sample sufficiently to accurately estimate pollinator SR, which is known to be hard to thoroughly sample especially over a small number of years (Russo et al., 2015). Increased sampling effort would allow more robust analyses of treatment effects across sites in future.

Bumblebees and solitary bees differed in their response to treatment, as also found by others (Kleijn and van Langevelde, 2006; Scheper et al., 2015): bumblebee SR showed no response to treatment, whereas solitary bee SR was higher in the AF treatment in some years at three of the six study sites. In agreement with other studies, we found different solitary bee SR responses in grassland compared to arable land. One of the pasture sites with increased SR in the AF treatment (site CE) also had the highest recorded amount of SNH in the surrounding landscape, concurring with findings that agri-environmental management (AEM) in grassland has the greatest effect on solitary bee SR in landscapes with more SNH (Concepción et al., 2012 - but see Kleijn and van Langevelde, 2006). Conversely, the arable site that showed a treatment effect (site WH) was in a highly homogenous, intensively-farmed region and had the least amount of SNH around it. This is in line with studies showing that AEM in arable landscapes had the greatest effect on solitary bee SR when there was little SNH in the surrounding landscape and where the management created large local contrast in resources (Concepción et al., 2012; Holzschuh et al., 2007; Scheper et al., 2015). The silvoarable system at WH provided great floral and structural diversity in the tree rows, thereby creating a large ecological contrast: this was likely to be the driver of the observed SR increase here.

The third site to show increased solitary bee SR in the AF treatment was another pasture site (WAF), but this one was in a very intensively-farmed landscape with little SNH. It is possible that here, the increased solitary bee SR may have been partly due to the fact that the site was un-grazed and well-established (Table A.1), allowing the tree rows to develop a structurally complex understorey that persisted from one year to the next (Buri et al., (2014) found cumulative (over time) positive effects of uncut grass refugia on wild bee SR). Furthermore, it had the largest contrast in within-field plant SR of any site, with over three times greater plant SR in the AF treatment: we found that, across all sites, solitary bee SR was positively correlated with plant SR so this may also have contributed to the observed difference in solitary bee SR at WAF. This correlation between solitary bee and plant SR is in agreement with other findings (Isbell et al., 2017; Lichtenberg et al., 2017; Sutter et al., 2017) and suggests that the treatment effect on SR was due to the higher plant diversity in these systems. This once again highlights the importance of careful design of AF systems to achieve the greatest possible increase in ecosystem service provision and biodiversity conservation.

4.3 Pollination service

The 2012 phytometer experiment showed higher seed set and thus greater pollination service in AF treatments, which is most likely to be due to the higher abundance of insect pollinators in AF treatments. Our findings are in line with previous studies linking insect pollinator abundance to pollination service (Winfree et al., 2015; Woodcock et al., 2019). The higher solitary bee SR in some of the AF treatments may also have contributed, as species richness has been shown to support pollination service (Albrecht et al., 2012; Dainese et al., 2019; Eeraerts et al., 2019) although its contribution to service delivery is inferior to that of abundance (Kleijn et al., 2015).

The phytometer results were inconsistent across the two years, although it is likely that the fieldwork issues in 2013 and experimental design were partly responsible, resulting in a very poor quality dataset. The large difference in seed set in the two years is likely to have been because in 2012 there was one plant per position whereas in 2013 there were two plants per position. As *E. californica* is self-incompatible, using a single plant per position is likely to have limited pollen availability in 2012. Also, in 2013 the distance between phytometers was smaller in MC treatments at two of the three sites (and equal in the third – hence its strong correlation with treatment in the proposed global model, Table B.12). As seed set has been shown to increase at higher flower densities (Dauber et al., 2010; Seifan et al., 2014) the distance between phytometers may have caused density-dependent effects on pollination, resulting in higher seed set where phytometers were closer together. Other variables likely to contribute indirectly to pollination (e.g. distance to the nearest hedgerow, field boundary area) were also correlated with treatment in the 2013 proposed global model (Table B.12) and were shown to be more important than, or as important as, treatment in the PCA. As a result, we cannot confidently ascribe the higher seed set in MC to any one variable and we suggest re-doing the phytometer experiment to confirm the presence and direction of any treatment effect. However, we remain confident in the conclusions drawn from the 2012 phytometer data.

5. Conclusions

This work presents strong empirical evidence that UK AF systems can support greater numbers of wild insect pollinators, greater pollination service and, at some sites, greater wild bee species richness. This could benefit both wild plant populations and insect pollinated agricultural crops in areas near AF systems. In Europe there is growing interest in the implementation of modern AF systems and this study provides robust evidence of its benefits to pollinators. These findings, taken together with evidence that AF systems can also produce more biomass per unit area than MC systems (Isbell et al., 2017; Sereke et al., 2015), means that AF systems may have a part to play in the sustainable intensification of agriculture. Our study adds to the body of evidence supporting the uptake of AF in temperate intensive farming systems. Our work also highlights that the provision of additional ecosystem services – *i.e.* ecosystem services other than biomass production – should be considered at the design stage of new AF systems to ensure the greatest possible benefit is realised.

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Declaration of interest

The authors declare they have no conflicts of interest.

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Figures

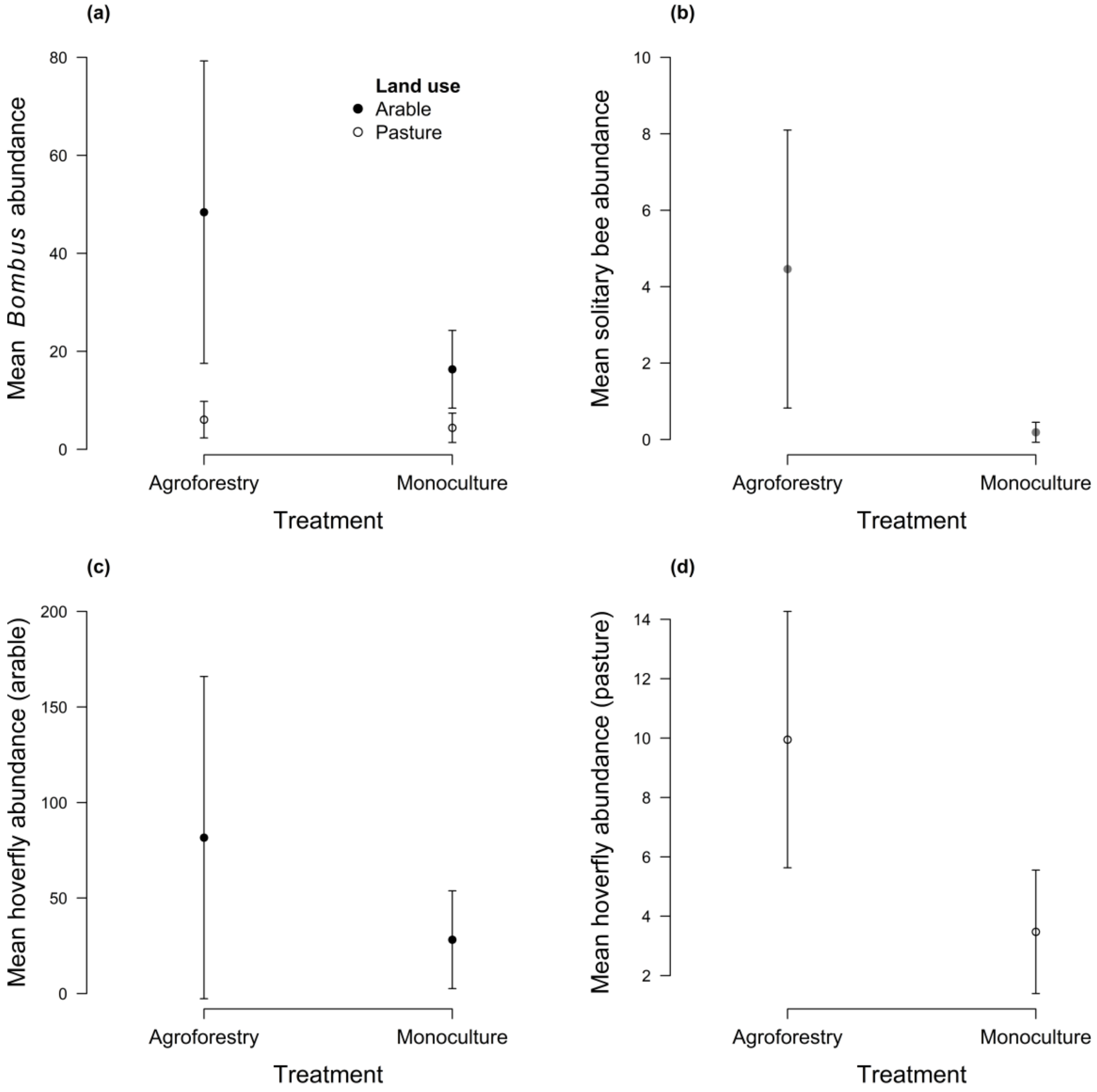

Figure 1 Abundance of wild pollinating insects from transect data. ● = arable land; ○ = pastureland; ● = both land use types. (a) Mean bumblebee abundance and 95% CIs; (b) Mean solitary bee abundance and 95% CIs; (c) and (d) hoverfly abundance was much higher in arable than pasture systems and these are therefore shown separately: (c) mean hoverfly abundance and 95% CIs, arable systems (figure shows mean abundance across both arable sites, hence the overlapping confidence intervals; however, model output shows strong evidence of a treatment effect in arable systems); (d) mean hoverfly abundance and 95% CIs, pasture systems.

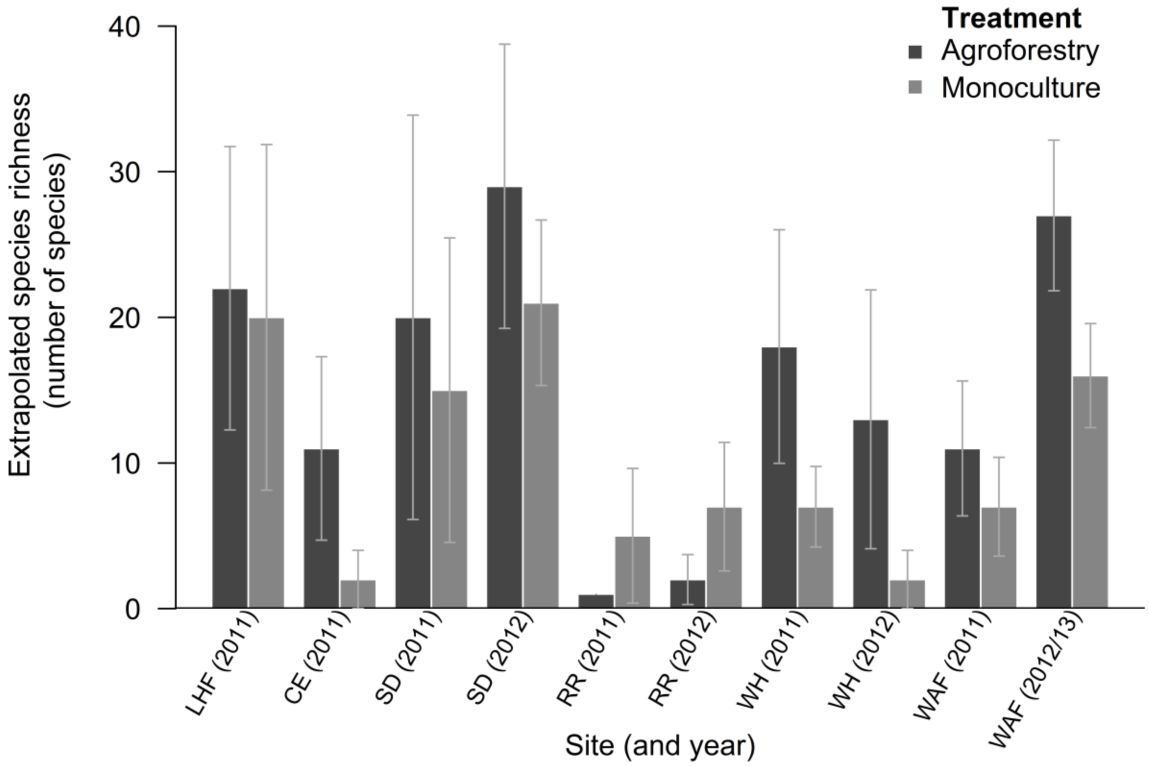

Figure 2 Species richness (extrapolated to 14 samples) of solitary bees at each site. Bars show 95% confidence intervals. For site details see Table A.1.

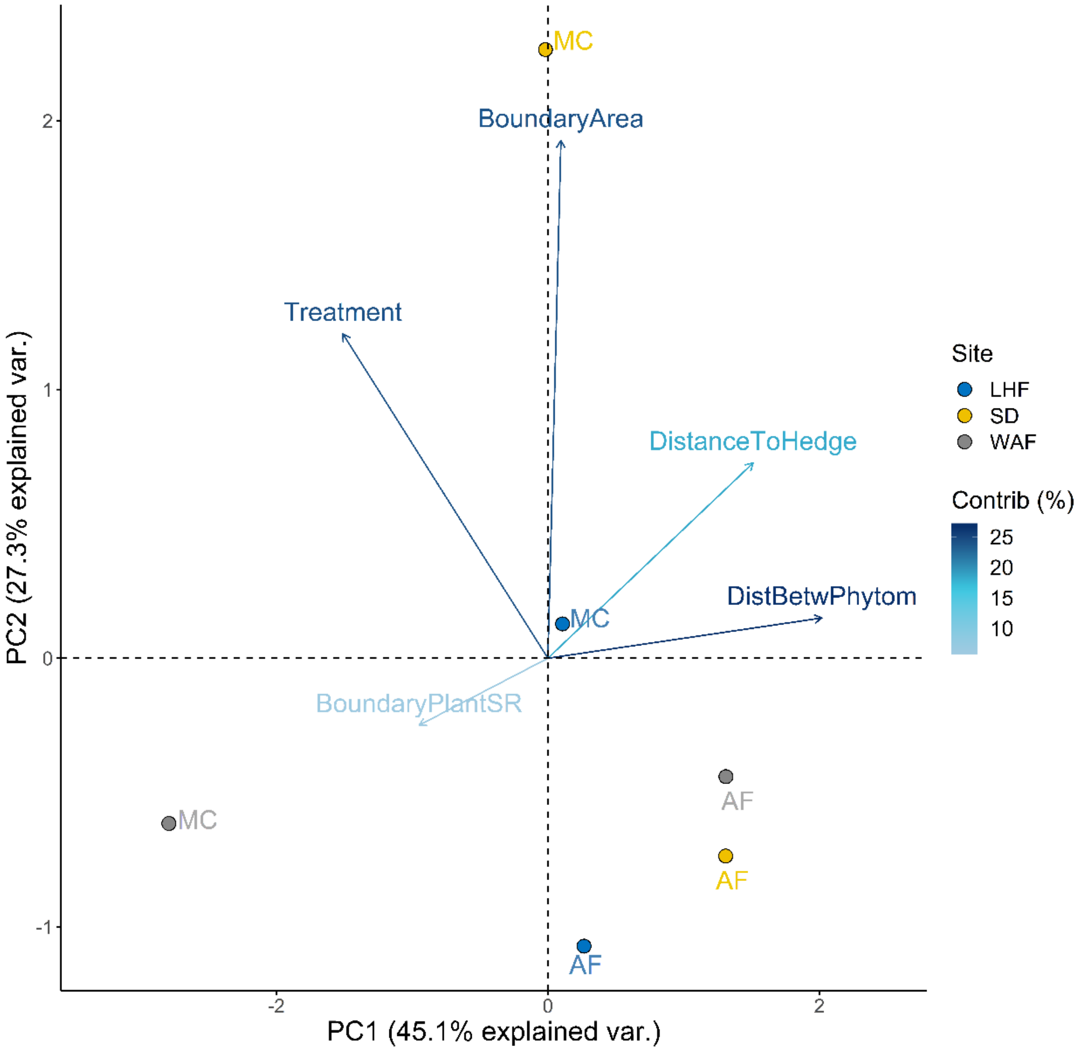

Figure 3 PCA loading plot of 2013 phytometer data. Variables are coloured according to their total contribution (%) to PC1 and PC2 combined. Variable names as follows: tmt, treatment; bound.area = total uncropped area (i.e. hedgerows, field margins) around field; hedg.dist = distance from the transect to the nearest boundary hedgerow; distbetw = the shortest (diagonal) distance between phytometer plants; ipBSR = species richness of insect-pollinated plants in field boundary.

Tables

Table 1 ABUNDANCE. Model-averaged parameter estimates from models relating wild pollinating insect abundance to environmental variables. For each pollinator group, regression coefficients (β, standardized at SD = 0.5) are averages of β_i across all models in the top model set, weighted by the Akaike weight w_i of each model in the top model set (Burnham and Anderson, 2002). w_i best = Akaike weight of the best model from each top model subset. Calculations for β only include β_i from models in which a given parameter appears (natural average method). Values in brackets are 95% confidence intervals. Relative variable importance (w_{ip}) is the sum of w_i across all models including that variable (Burnham & Anderson 2002). Variables with the greatest importance for each pollinator group have w_{ip} in bold. NA indicates that the corresponding parameter was not included in any of the top models for that pollinator group. For details of all models in each top model set, see Appendix B.

	Model averaged values					
	Bumblebee abundance◊		Solitary bee abundance◊		Hoverfly abundance◊	
w_i best:	0.45		0.58		0.49	
Parameter*	β	w_{ip}	β	w_{ip}	β	w_{ip}
(Intercept)†	1.9522 (1.415, 2.489)		0.3919 (0.161, 0.622)		2.6476 (1.882, 3.413)	
treatment	-0.8861 (-1.323, -0.449)	**1.00**	-1.0427 (-1.380, -0.705)	**1.00**	-1.0648 (-1.833, -0.297)	**1.00**
landuse	-2.0318 (-3.210, -0.854)	**1.00**	-0.1165 (-0.852, 0.619)	0.22	-1.4099 (-2.304, -0.515)	**1.00**
treatment :landuse	1.0529 (0.264, 1.842)	**1.00**	0.5877 (-0.316, 1.492)	0.08	0.5919 (0.306, 0.878)	0.32
sun	-0.5191 (-0.964, -0.074)	0.83	NA	NA	NA	NA
hedg.dist	-0.6943 (-1.250, -0.138)	0.79	-0.8551 (-1.305, -0.405)	**1.00**	NA	NA
bound.area	-0.2389 (-0.732, 0.254)	0.17	0.2164 (-0.171, 0.604)	0.12	-0.2916 (-0.428, -0.155)	0.20
days.sq	NA	NA	-0.1350 (-0.440, 0.170)	0.09	2.2711 (1.188, 3.354)	**1.00**
snh	NA	NA	-0.9477 (-1.458, -0.437)	**1.00**	NA	NA
treatment :snh	NA	NA	1.1564 (0.568, 1.745)	**1.00**	NA	NA

† Intercept shows estimated effect when treatment = agroforestry and land use = arable

* Parameters as follows: treatment = agroforestry or monoculture; landuse = land use, arable or pasture; treatment:landuse = interaction between the two previous two parameters; sun = percentage of transect that was sunny; hedg.dist = distance from the transect to the nearest boundary hedgerow; bound.area = total uncropped area (*i.e.* hedgerows, field margins) around field; days.sq = quadratic term, $date^2$, where date is the number of days since 1st March; snh = percentage of semi-natural habitat in 1km buffer round each field; treatment:snh = interaction between treatment and snh. NA values indicate that the variable was not in the model set.

[◊] Bumblebee and hoverfly transect data is from 5 sites in 2011, 4 sites in 2012 and 1 site in 2013 (6 sites across all years); solitary bee transect data is from 6 sites in 2011, 4 sites in 2012 and 1 site in 2013 (6 sites across all years). See Table A.3 for site-by-year data collection details.

Table 2 SPECIES RICHNESS. Model-averaged parameter estimates from models relating bumblebee species richness and square root of solitary bee species richness to environmental variables at six sites. For a full explanation of this table see legend for Table 1. For details of all models in each top model set, see Appendix B.

	Model averaged values			
	Bumblebee species richness[◊]		Solitary bee species richness[◊]	
w_i best:	0.35		0.30	
Parameter*	β	w_{ip}	β	w_{ip}
(Intercept)[†]	0.9474 (0.646, 1.249)		3.3742 (2.633, 4.115)	
treatment	NA	NA	-0.6806 (-1.416, 0.055)	0.27
n.hedg.bound	0.5276 (-0.021, 1.077)	0.51	1.3360 (0.300, 2.372)	0.15
hedg.dist	NA	NA	1.1926 (-0.081, 2.467)	0.31
snh	NA	NA	-0.9001 (-2.289, 0.489)	0.13
bound.area	-0.3945 (-1.069, 0.280)	0.30	NA	NA

†* Footnotes as for Table 1, with the addition of n.hedg.bound = number of hedged boundaries around field.

[◊] Bumblebee pan trap data is from 5 sites in 2011, 4 sites in 2012 and 1 site in 2013 (6 sites across all years); solitary bee pan trap data is from 6 sites in 2011, 4 sites in 2012 and 1 site in 2013 (6 sites across all years). See Table A.4 for site-by-year data collection details.

Table 3 Seed set. Model-averaged parameter estimates from models for models relating phytometer seed counts in 2012 to environmental variables. w_i best = Akaike weight of the best model from the top model subset. For a full explanation of this table see legend for Table 1. For details of all models in the top model set, see Appendix B.

	Model averaged values	
	Seed count 2012[◊]	
w_i best:	0.68	
Parameter*	β	w_{ip}
(Intercept)[†]	-0.1088 (-0.666, 0.448)	
treatment	-1.7241 (-2.530, -0.918)	**1.00**
hedg.dist	-1.8241 (-2.908, -0.740)	**1.00**
bound.area	-0.4663 (-1.313, 0.381)	0.32

†* Footnotes as for Tables 1 & 2.

[◊] Seed count is average number of seeds per fruit. 2012 phytometer data is from 1 pasture and 2 arable sites.

Table 4 Summary of analyses in which there was strong evidence of a treatment effect.

Taxon or dataset[‡]	Metric	Result[†]	Magnitude of result [Δ]	Land use[*]
Bumblebees	abundance	AF > MC	2.4	a
Hoverflies	abundance	AF > MC	2.0	a, p
Solitary bees	abundance	AF > MC	2.0	a, p
Solitary bees	species richness	AF > MC at 40% of site-by-year samples	10.5	a, p
Solitary bees & plants	species richness correlation	+	NA	a, p
phytometer data, 2012	seed set	AF > MC	4.5	a, p

‡ All pollinator taxa were sampled in both 2011 and 2012. Plant species richness was sampled in the first year that data collection was carried out in a field.

† Result shows direction of relationship between AF (agroforestry) and MC (monoculture) treatments, or direction of correlation (+ = positive).

[Δ] Magnitude indicates effect size, or how many times higher one value was than the other: *i.e.* bumblebee abundance was 2.4 times higher in AF treatments than MC treatments (in arable land). The value for solitary bee species richness is the average magnitude across instances where SR was significantly higher.

*Column indicates in which type of land use the result was found: a = arable, p = pasture.