The benefits of hedgerows for pollinators and natural enemies depends on hedge quality and landscape context

Article

Accepted Version

Published version at: http://www.sciencedirect.com/science/article/pii/S0167880917302918
To link to this article DOI: http://dx.doi.org/10.1016/j.agee.2017.06.048

Publisher: Elsevier

The benefits of hedgerows for pollinators and natural enemies depends on hedge quality and landscape context

Michael P. D. Garratt, Grace D. Senapathi, Duncan J. Coston,

Simon R. Mortimer and Simon G. Potts

Centre for Agri-Environmental Research, School of Agriculture, Policy and Development, University of Reading, UK.

Corresponding author: Dr Michael P. D. Garratt
Centre for Agri-Environmental Research (CAER),
School of Agriculture, Policy and Development,
University of Reading, RG6 6AR, UK.
Tel (Uni): +44 (0)1183786149
Email: M.P.Garratt@reading.ac.uk
Running title: Hedgerows, pollinators and predators

Keywords

Ecosystem services, hedgerows, pollination, pollinators, pest regulation, natural enemies, ecological intensification

Abstract

Ecological intensification advocates the harnessing of regulating and supporting ecosystem services to promote more sustainable food production, and this relies on effective management of non-cropped habitats. Hedgerows are an important component of the landscape in many farming systems across the world, management of which provides a potential mechanism to enhance ecological intensification. Here we investigate the value of hedgerows in Southern England as a source of functionally important taxa, and how hedgerow quality and local landscape composition impact on their potential contribution to sustainable agriculture in arable landscapes. We show that hedgerows are a source habitat for many natural enemies which spill over into neighbouring fields, and that hedgerows provide a valuable forage resource and corridor for movement of pollinators. Hedgerow quality effects these benefits and continuous unbroken hedgerows, with a high diversity of woody species, are more valuable for the provision of bumblebees and Linyphiid spiders, while the presence of trees within the hedgerow supports Lycosid spiders. Floral resources, beyond the woody hedgerow species themselves, are also a key forage resource for hoverflies. The impact of these hedgerows on invertebrate abundance is moderated by local landscape, and hedgerows are a more valuable forage resource for pollinators in more intensely managed landscapes. Our study shows that in order to support abundant and a broad range of natural enemies and pollinators in agricultural landscapes, both hedgerows and local semi-natural habitats need to be protected and managed. The benefit of hedgerows, as a habitat for functionally important taxa depends on hedgerow quality and management practices such as avoiding gaps, high hedge species diversity and maintaining an abundant understory of plants, can improve their value for ecological intensification.

Introduction

In order to address the increasing demand for food while simultaneously reducing the environmental impacts of agriculture, ecological intensification advocates the replacement of anthropogenic inputs and/or enhancement of crop productivity, by including regulating and supporting ecosystem service management in agricultural production (Bommarco *et al.*, 2013). Agricultural production itself, however, has been a key driver of declining biodiversity in the wider landscape (Matson *et al.*, 1997) simultaneously reducing the capacity of this biodiversity to provide ecosystems services such as crop pollination and pest regulation. Non-cropped land and semi-natural habitat within agricultural landscapes have been shown to be reservoirs of biodiversity, including functionally important taxa that provide services underpinning crop production at local and landscape scales (Bianchi *et al.*, 2006; Chaplin-Kramer *et al.*, 2011; Kennedy *et al.*, 2013; Shackelford *et al.*, 2013), with spill over from these natural areas into cropped habitats in evidence (Garibaldi *et al.*, 2011; Blitzer *et al.*, 2012; Macfadyen and Muller, 2013; Woodcock *et al.*, 2016). The spatial makeup of landscapes is also important and it is not simply the area of valuable habitat components that supports abundant biodiversity but also the high heterogeneity and connectivity within the landscape promotes flow, stability and delivery of biodiversity based ecosystems services (Mitchell *et al.*, 2013; Rusch *et al.*, 2013), and hedgerows can make an important contribution to this. Maximising the positive impacts of semi-natural habitats on key service providing taxa, and their capacity to deliver ecosystem services, is therefore an important component of sustainable agricultural management and a corner stone of ecological intensification.

Hedgerows are common linear semi-natural features in lowland agricultural landscapes across the world (Hannon and Sisk, 2009; Morandin and Kremen, 2013; Dainese *et al.*, 2016; Dondina *et al.*, 2016; Lacoeuilhe *et al.*, 2016; Ponisio *et al.*, 2016). They are a particularly ubiquitous feature of the UK countryside, with more than 450,000 km of hedgerows in England alone (Norton *et al.*, 2012). Hedgerows provide a valuable habitat and food resource for biodiversity including invertebrates (Amy *et al.*, 2015; Staley *et al.*, 2016), plants (Critchley *et al.*, 2013) and other wildlife (Staley *et al.*, 2012; Dondina *et al.*, 2016) and may provide an important mechanism for increasing the abundance of functionally important taxa and improving the permeability of agricultural landscapes allowing more access to crop fields (Haenke *et al.*, 2014). In light of this, hedgerows are a priority habitat across Europe and support for their management is provided to land managers through agri-environment schemes (Natural England, 2013).

Hedgerows can provide a valuable habitat for functionally important taxa including pollinators (Hanley and Wilkins, 2015; Sardiñas and Kremen, 2015; Ponisio *et al.*, 2016) and natural enemies (Amy *et al.*, 2015). There is some emerging evidence that these taxa spill over into adjacent crop fields (Morandin and Kremen, 2013; Haenke *et al.*, 2014; Morandin *et al.*, 2014; Morandin *et al.*, 2016) where they may provide services. The manner in which hedgerows are managed has significant implications on their value as a habitat resource (Maudsley, 2000; Staley *et al.*, 2012; Amy *et al.*, 2015; Staley *et al.*, 2016) and this presents an opportunity for farmers to optimise the management of hedgerows to increase the benefits they provide to food production, as well as a habitat for wildlife.

To develop the potential contribution of hedgerows towards ecological intensification, it is important to understand which taxa they enhance and whether this benefit translates into improved ecosystem services for farmers. Identifying the optimal management of hedgerows to support taxa underpinning crop production, and understanding how hedgerows function within a wider context could enable the development of management practices to support sustainable food production. The aims of the present study were to: 1) measure the effect hedgerows have on the spill-over of functionally important taxa into cropped fields; 2) understand how hedgerow management and quality (based on structure and plant diversity) affects the composition and spill-over of pollinators and natural enemies; and, 3) determine how hedgerows and surrounding semi-natural landscape components interact to influence the abundance of functionally important taxa found in crop fields.

Materials and methods

Study sites

In 2014, sixteen field sites were selected in four, 25km x 25km landscape blocks in Southern England (Fig 1a). The climate in this region is maritime temperate and agriculture is predominantly conventional arable production with cereals in rotation with oilseed rape and field beans. Field sites for this study included a hedgerow adjacent to a crop of winter wheat (Fig 1b.). These hedgerows had been previously classified as “Good” or “Poor” quality based on data collected as part of a Department for the Environment and Rural Affairs (Defra) condition assessment (Defra, 2007) carried out during a previous study (Chiltern Conservation Board, 2008, Hedgerow Survey 2006 and 2007). Good quality hedges were defined as those containing more than three woody species within the 75m study section, with a solid structure with no gaps bigger than 2 meters. Poor quality hedges had fewer than three woody species, had poor overall structure with variable height and width with gaps greater than 2m, and showed little evidence of maintenance. The local landscape surrounding these hedgerows was characterized at a 500m radius considering the % area of semi-natural habitat based on the UK Government’s Priority Habitat Inventory (Natural England, 2014) which includes deciduous woodland, good quality semi-improved grassland, lowland calcareous grassland and lowland meadow. A 500m radius was chosen because it is likely to capture responses for the diverse groups of both natural enemies and pollinators being considered, and is generally relevant for management at the farm scale. Within each study region there were four hedgerows, two good quality and two poor quality, with one located in an area of high semi-natural habitat (>5% with a range of 9.89 to 41.97% across sites) and one in an area of low semi-natural habitat (<5% with a range of 0.0 to 4.71% across sites). Initial selection of sites was carried out using ArcGIS10.1 followed by ground-truthing to determine final study sites.

Invertebrate sampling

At each study hedge, three 50m transects, running perpendicular to the field edge and hedgerow, 25m apart and at least 50m from other field boundaries were marked out. Invertebrates were sampled using pitfall traps placed at 0, 10, 25 and 50m along each transect into the wheat field to assess abundance (activity density) of ground active natural enemies. Pitfall traps, with a 95mm diameter containing dilute anti-freeze solution, with a rain cover were placed out for a period of 10 days. In order to capture spring and summer activity of natural enemies, two rounds of pitfall sampling was carried out, the first in late April / early May 2014 and the second in mid-June 2014. After collection, pitfall trap contents were stored at -20^{o}C and then natural enemies were counted and identified to broad functional groups including Carabids, Staphylinids, Linyphiid spiders, Lycosid spiders, Coccinellids, Centipedes and Opiliones.

Aphid population density was sampled in the wheat crop three times during the season, at stem elongation in early May, flowering in early June and dough development in early July 2014. As with pitfall trapping, aphid populations were estimated at sampling locations located at 0, 10, 25 and 50m along each transect. At each sampling location, 25 tillers were examined and the number and species of aphids recorded. The number of parasitoid mummies was also counted.

The abundance of bumblebees, hoverflies, honeybees and solitary bees was recorded along transects running parallel to the hedgerow, at 0m,10m and 50m into the field. Each transect was 75m long and divided into three, 25m sub sections. On the day of pollinator surveys, each sub-section was walked slowly for a period of 5 minutes and all bees and hoverflies 2m either side of the observer were recorded. For the transect immediately adjacent to the hedgerow, whether pollinators were observed visiting flowers on the hedgerow itself or flowers which were part of the non woody understorey of the hedge bank was also noted. All surveys were carried out in low wind conditions and in temperatures in excess of 15^{o}C. Three rounds of pollinator surveys were carried out at each field site, the first in mid-May, the second in mid-June and the final survey in mid-July 2014.

Hedgerow characterisation

At the time of pollinator surveys a floral resource survey was carried out along each of the hedgerows. At the base of each transect a 0.5m by 0.5m quadrat was held up to the hedge. Based on height, the hedge was divided into thirds and a quadrat was held up to the lower section, mid-section and upper section of the hedge. A photograph was taken of each quadrat and back at the laboratory the percentage coverage of each quadrat with open flowers was visually estimated to the nearest 2%. This was done three times during the season at the same time as pollinator surveys.

In October 2014, a visit was made to all experimental hedgerows to collect further data on hedgerow characteristics. On the 25m hedge section at the base of each transect, hedge height and width were estimated to the nearest 25cm based on three independent measures per section. Then to assess hedge continuity, the percentage extent of gaps in woody species was noted (% coverage); and whether there were any gaps greater than 5m present (yes/no) was recorded. The number of species of woody hedgerow plants were recorded and an assessment made of how recently the hedge was cut (<2yrs, 2-10yrs). Hedgerow type was characterised for each section as 'bank', 'shrub', 'tree' or 'tree and shrub' in line with Defra's condition assessment (Defra, 2007). In addition, two 1m by 1m quadrats were placed on the ground on either side and towards the centre of each hedge section to assess understory plant composition. The number of non-grass plant species within the quadrat was recorded and summed from both sides to get a measure of species richness.

Data analysis

Linear mixed effects models were used to investigate effects of hedge quality, percentage semi-natural habitat and distance into the field on natural enemies caught in pitfall traps. Data were log +1 transformed before analysis. 'Transect' within 'site' within 'block' within 'round' were included as nested random effects. Models were selected based on deletion of least significant variables using a likelihood ratio test. All models retained main effects and random effects during model comparisons and final model residuals were checked for normality and heteroscedasticity. Generalised linear mixed effects models with a poisson error structure were also used to investigate natural enemy, aphid and pollinator responses but model residuals were skewed and models often failed to converge. Linear mixed effects models using transformed data were superior.

The number of aphids observed on 25 tillers at each sample location was analysed in the same way as for natural enemy pitfall catches. In the first analysis, all aphid species were combined and then, as the most abundant species, *M. dirhodum* and *S. avenae* were analysed separately. Aphid percentage parasitism (as aphids + mummies/aphids * 100) was analysed using a generalised linear mixed effects models with a binomial error structure, otherwise main effects, random effects and model selection were the same as for previous models.

For analysis of pollinator survey data, counts were combined by broad taxonomic groups (honeybees, hoverflies, bumblebee and solitary bees) and a total bee response was also analysed. Linear mixed effects models were used with the same fixed and random effects as earlier models. Data were log +1 transformed as before to ensure data normality. To assess effects of hedge quality and landscape on pollinators and to improve data normality, counts were pooled within each transect and so distance into the field was removed from the model. To test for effects of distance into the field on pollinator abundance a separate linear mixed effects model was run where data were pooled by section, but to maintain the assumption of normal residuals and heteroscedasticity, only effects on hoverflies and total bees could be analysed. Pollinator foraging data were analysed using a linear mixed effects models and whether pollinators were visiting flowers associated with the hedgerow or understorey vegetation was compared. To reduce zero counts and improve data normality, data were pooled within transects and within sites, so transect and distance were removed as random effects in the analysis.

If a significant or near significant effect of hedge quality was found on any pest, natural enemy or pollinator taxa then additional analyses were carried out to determine what hedge factors could be driving this response. Linear mixed effects models were used with block, site, transect and round as nested random effects. Main effects tested included hedge type (bank, shrub, shrub and tree, tree), hedge height (nearest 25cm), hedge width (nearest 25cm), hedge continuity (% gaps), gaps >5m (yes/no), management frequency (<2yrs or 2-10yrs), hedge species richness, understory species richness and percentage flower cover. Given the correlation of hedge characteristics, these variables were investigated individually in separate models. To improve data normality, for bumblebees, data from transects were pooled so distance from the hedge was removed from the analysis. Linear mixed effects models were run using the 'nlme' package and generalised linear models using the 'lme4' package. All statistical analysis was carried out in R version 3.3.1 (R Core Development Team, 2013).

Results

A total of 4,741 Carabids, 2,247 Staphylinids, 2,213 Linyphiid spiders and 1,126 Lycosid spiders were collected in pitfall traps, other natural enemies including Coccinellids, centipedes and Opiliones were not caught in adequate numbers for analysis. The abundance of Lycosids, Linyphiids and Staphylinids was affected by distance into the field, with abundance decreasing with increasing distance from the hedgerow (Fig 2a) (Table 1.). For Lycosids the decline was pronounced with a drop of more than 80% from 7.79 (SE±1.56) per trap at the field edge to 0.91 (SE±0.22) at 50m. Although significant, the decline for Linyphiids was less, with a drop from 6.43 (SE±0.71) to 5.19 (SE±0.79) and for Staphylinids, 6.76 (SE±0.80) to 5.03 (SE±0.69), for the same distance. The interaction between distance and percentage semi-natural was also found to have significant effects on Staphylinids. Hedge quality significantly affected Linyphiids, with more found in traps associated with good quality hedgerows (6.54 SE±0.82) compared to poorer quality ones (4.98 SE±0.68). A near significant effect on Lycosids was also observed with 3.66 (SE±1.01) average catch per trap next to poor quality hedges and 2.21 (SE±0.49) next to good quality hedges. Local semi natural habitat also had a significant positive effect on Lycosids (Fig 2b).

No effect of distance (Estimate: -0.004, z = -1.17, p = 0.24), hedge quality (Estimate: -0.085, z = -0.48, p = 0.63) or semi-natural habitat (Estimate: 0.007, z = 1.04, p = 0.30) on percentage parasitism was found. *Metopolophium dirhodum* were the most abundant aphid species recorded, followed by *S. avenae* and *R. padi*. A significant effect of distance into the field on all aphids per tiller and *Metopolophium dirhodum* per tiller was found (Table 1.) with greater numbers towards the field edge (Fig 3a). Aphid populations were very low however, and the difference between densities at the edge and 50m into the field were not large (All aphids Edge: 0.27 [SE±0.03] 50m: 0.19 [SE±0.03], M. dirhodum Edge: 0.15 [SE±0.03] 50m: 0.12 [SE±0.02]). No significant effects of hedge quality or semi-natural habitat on aphid abundance were found (Table 1) (Fig 3b).

Overall 150 honey bees, 136 bumblebees, 140 solitary bees and 276 hoverflies were observed during this study. Total bees and hoverfly abundance was significantly greater on the hedgerow when compared to 10m and 50m away from the hedge (Table 1) (Fig 4a). A significant effect of percent semi-natural habitat on total bees was also found with a negative correlation between abundance and semi-natural habitat (Fig 4b). More than twice as many bumblebees were observed on transects near good quality hedges (1.31 SE±0.35) compared to poor quality ones (0.58 SE±0.16) and this effect was significant (Table 1).

Eighteen woody hedgerow species were recorded during the course of the study as well as many more understorey plants. Following analyses of the effects of individual hedgerow characteristics on responsive taxa, the abundance of Linyphiids was found to be negatively associated with discontinuous hedges with a high proportion of gaps ($F_{1,63}$ = 5.88, p = 0.018) or hedges with gaps greater than 5m ($F_{1,63}$ = 6.19, p = 0.016). Also hedges that remained uncut for more than 2 years supported more Linyphiids ($F_{1,63}$ = 8.30, p = 0.0084). Lycosids were significantly affected by hedge type ($F_{1,63}$ = 3.65, p = 0.017) with greater numbers associated with 'tree' and 'tree & shrub' hedges compared to 'shrub' hedges alone. No significant effects of individual hedgerow characteristics on bumblebees were found.

Considering the foraging of pollinators on hedgerows, hoverflies were found visiting understorey flowers significantly more than flowers on plants within the hedgerow ($F_{1,15}$ = 8.85, p = 0.017) with 78.8% of visits observed to plants in the understorey. No such effects were seen for solitary bees ($F_{1,15}$ = 3.62, p = 0.077), bumblebees ($F_{1,15}$ = 0.82, p = 0.38) or honeybees ($F_{1,15}$ = 1.65, p = 0.22).

Discussion

Hedgerows can provide key resources for functionally important taxa in intensive agricultural landscapes but the extent of this benefit depends on the characteristics of the hedgerow and the landscape context in which the hedgerow is found. Spiders are important natural enemies of crop pests including those of cereal crops (Sunderland *et al.*, 1986; Lang, 2003) and, like many other natural enemies, their abundance depends on local landscape context (Sunderland and Samu, 2000). Our study shows that hedgerows provide an important reservoir of spiders which spill over into neighbouring wheat fields. This is particularly true for Lycosids with declines in activity density of more than 80% between the field edge and 50m into the field. The abundance of Lycosid spiders also increased in wheat fields surrounded by landscapes with a high proportion of semi-natural habitat, and they also benefit from the presence of trees within the hedgerows. The abundance of Linyphiids found in wheat fields is greater next to better quality hedgerows, in particular those which are continuous without large gaps. The prey of these two groups of spiders differ with Lycosid spiders being rather generalist (Nyffeler and Sunderland, 2003), while Linyphiid spiders will predate invertebrates active in the canopy (e.g. aphids) (Sunderland and Samu, 2000). Depending on the pests associated with a crop, management to promote abundance of one or the other groups of spiders could be targeted, by either maintaining a high number of unbroken hedgerows in the landscape or ensuring an abundance of local patches of semi-natural habitat such as woodland.

Staphylinids are an important component of the ground-active natural enemy community in arable systems (Dennis and Sotherton, 1994). They are particularly common in disturbed agricultural landscapes (Bohac, 1999; Schmidt *et al.*, 2003), and our study shows that hedgerows which permeate these landscapes are an important source of such populations, but average catch of Staphylinids declined by only 25% at 50m from hedgerows. Therefore their high mobility allows them exploit arable fields to some distance, or certain species are able to persist within the cropped habitat throughout the season. In our study, carabid beetles appear unresponsive to hedge proximity, hedge quality and local landscape. Carabids are a very diverse group able to utilise a wide range of habitats, and some common species are known to persist in intensive arable crop fields which may explain the lack of response to hedges (Kromp, 1999). Species level data may allow possible effects on individual species to emerge. Aphid numbers were very low during this study, with an average of 0.22 aphids observed per tiller, which is well below action thresholds (Larsson, 2005) although a shallow decline away from the hedgerows in some species was observed. It maybe that the direct impacts of these more abundant natural enemies would be observed at greater pest densities only, and maintaining abundant predator populations in the longer term may reduce the frequency with which some pests reach action thresholds. However, the potential disbenefits of landscape features such as hedgerows at providing a resource for pests also needs to be taken into account although the relationship between pests and natural enemies will change with pests density and greater abundance and diversity of natural enemies consistently reduces aphid populations (Schmidt *et al.*, 2003; Rusch *et al.*, 2013; Ramsden *et al.*, 2016).

Hedgerows provide an important forage and dispersal resource for many pollinator species (Hannon and Sisk, 2009; Morandin and Kremen, 2013; Sardiñas and Kremen, 2015). However, we show that the value of these hedgerows depends on hedgerow quality, with more than twice as many bumblebees observed on good quality hedgerows. Furthermore, foraging of hoverflies on these hedgerows tended to be on the flowering plants associated the hedgerow understory rather than on the hedgerow species themselves. Flowering plants are known to be a valuable resource, particularly for hoverflies and parasitoids (Ramsden *et al.*, 2015), and they are impacted by long-term hedgerow management (Maudsley, 2000; Critchley *et al.*, 2013; Staley *et al.*, 2013). The utilisation of floral resources associated with hedgerows by different species may change through the year however as different plant species are in flower. For example, very early in the season, blackthorn is an important nectar and pollen source, followed by hawthorn, dog rose and then bramble (Maudsley, 2000). Thus it is the diverse hedgerow in combination with the immediate vegetation margin, which provides pollinators with a forage resource.

The abundance of pollinators observed on hedgerows was dependent on local landscape context, with greater numbers seen in areas with a lower local proportions of semi-natural habitat. This indicates hedgerows may be a more valuable forage resource for bees in more intensive landscapes depauperate of semi-natural habitat. This is a phenomenon known as ‘ecological contrasts’ and has implications for the importance of hedgerows in different contexts (Tscharntke *et al.*, 2005; Kleijn *et al.*, 2011). The value of bees and hoverflies as crop pollinators of arable crops such as oilseed and field bean grown in this study region (Garratt *et al.*, 2014; Kleijn *et al.*, 2015) coupled with the observed spill over of these pollinators from hedgerows into neighbouring fields (Morandin and Kremen, 2013; Morandin *et al.*, 2016) points to potential gains in crop production from maintaining good quality hedgerows in agricultural landscapes.

Based on the responses shown by pollinators and natural enemies to certain hedgerow characteristics, management practices could be implemented to improve the quality of hedgerows for both pollinators and natural enemies. Woody species diversity can be increased by allowing hedges to develop and recruit new species over time or by planting core hedge species such as hawthorn, blackthorn and hazel. Hedge laying will also help to reduce the number and size of gaps in hedgerows while new hedge planting will increase their density in the landscape and if this is targeted, then the benefits of spill over can be maximised by ensuring no cropped area of the field is more than a minimum distance from any hedgerow. Specifically the presence of trees within the hedgerow benefited Staphylinids and maintaining these trees could be considered as a deliberate management strategy. The hedge understorey also provides a key floral resource for pollinators so reduced mowing and herbicide application at key times will maintain the benefit these plant species can provide. Agri-environmental policy already considers management of hedgerows and some of these management practices are currently included in the UK Countryside Stewardship scheme, including 'gapping-up', 'laying' and 'tree planting' (Countryside Stewardship: Hedgerows and Boundaries Grant Manual, 2017). However the reasons for implanting such practices is not made clear, this and similar research could be used to underpin more targeted management strategies based on the particular benefits individual farmers or particular regions are looking to achieve.

Our study shows the potential benefits of hedgerows for pollinators and natural enemies in agricultural landscapes. Ultimately, investment in maintaining and managing non-cropped land in agroecosystems involves a trade-off between the benefits provided by these components of the landscape, the loss of production area, and the cost of management (Morandin *et al.*, 2016). As we begin to quantify the economic value provided by beneficial taxa such as pollinators (Gallai *et al.*, 2009; Garratt *et al.*, 2016) and pest regulators (Losey and Vaughan, 2006; Zhang and Swinton, 2009) and we relate this to abundance, we can begin to estimate the potential impact of landscape features such as hedgerows. In the long run this can be used to inform economic decisions and investment in non-cropped habitats and investment can be made to match the benefits they provide to crop productivity. However the wider social, environmental and ecological benefits of hedgerows and their value as wildlife refuges, benefits for soil protection, contribution to landscape aesthetic and many other values cannot be ignored.

Conclusion

Areas of semi-natural habitat within the landscape are sources of functionally important taxa, including pollinators (Garibaldi *et al.*, 2011) and natural enemies (Chaplin-Kramer *et al.*, 2011), but it is becoming increasingly clear that the distribution, configuration and quality of these non-farmed components influences the extent of these benefits (Mitchell *et al.*, 2013). Here we show that hedgerows are a key component of these landscapes, but the quality of these hedgerows affects the response shown by some beneficial taxa, while others are affected by characteristics of the local landscape. Given that diverse communities of natural enemies provide better pest regulation (Schmidt *et al.*, 2003) and different arable crops are pollinated by different functional groups of pollinators (Garratt *et al.*, 2014), maximising the abundance of diverse invertebrate communities through the life of a cropping system is likely to strengthen the contribution of both services to production and yield stability. Our study shows that continuous, unbroken hedgerows with diverse woody species and a florally rich understorey within a landscape containing a high proportion of local semi-natural habitat could maximise the provision of ecosystem services provided by pollinators and natural enemies.

Acknowledgements

This research was funded by the European Community's Seventh Framework Programme under grant agreement no 311781, LIBERATION Project (www.fp7liberation.422 eu). We would like to thank all the farmers who allowed us to carry out the research on their land and we would also like to thank all the research technicians involved in the project, particularly Louise Truslove and Rebecca Evans.

References

Amy, S.R., Heard, M.S., Hartley, S.E., George, C.T., Pywell, R.F., Staley, J.T., 2015. Hedgerow rejuvenation management affects invertebrate communities through changes to habitat structure. Basic and Applied Ecology 16, 443-451.

Bianchi, F., Booij, C.J.H., Tscharntke, T., 2006. Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. Proceedings of the Royal Society B: Biological Sciences 273, 1715-1727.

Blitzer, E.J., Dormann, C.F., Holzschuh, A., Klein, A.-M., Rand, T.A., Tscharntke, T., 2012. Spillover of functionally important organisms between managed and natural habitats. Agriculture, Ecosystems & Environment 146, 34-43.

Bohac, J., 1999. Staphylinid beetles as bioindicators. Agriculture, Ecosystems & Environment 74, 357-372.

Bommarco, R., Kleijn, D., Potts, S.G., 2013. Ecological intensification: harnessing ecosystem services for food security. Trends in Ecology & Evolution 28, 230-238.

Chaplin-Kramer, R., O'Rourke, M.E., Blitzer, E.J., Kremen, C., 2011. A meta-analysis of crop pest and natural enemy response to landscape complexity. Ecology Letters 14, 922-932.

Countryside Stewardship: Hedgerows and Boundaries Grant Manual. Published 1st February 2017. Accessable at: https://www.gov.uk/government/uploads/system/uploads/attachment_data/file/587391/cs-hedgerows-boundaries-grant-manual-2017.pdf

Critchley, C.N.R., Wilson, L.A., Mole, A.C., Norton, L.R., Smart, S.M., 2013. A functional classification of herbaceous hedgerow vegetation for setting restoration objectives. Biodiversity and Conservation 22, 701-717.

Dainese, M., Montecchiari, S., Sitzia, T., Sigura, M., Marini, L., 2016. High cover of hedgerows in the landscape supports multiple ecosystem services in Mediterranean cereal fields. Journal of Applied Ecology, n/a-n/a.

Defra, 2007. Hedgerow Survey Handbook A standard procedure for local surveys in the UK. Defra, London.

Dennis, P., Sotherton, N.W., 1994. Behavioural aspects of staphylinid beetles that limit their aphid feeding potential in cereal crops. Pedobiologia 38, 222-237.

Dondina, O., Kataoka, L., Orioli, V., Bani, L., 2016. How to manage hedgerows as effective ecological corridors for mammals: A two-species approach. Agriculture Ecosystems & Environment 231, 283-290.

Gallai, N., Salles, J.M., Settele, J., Vaissiere, B.E., 2009. Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. Ecological Economics 68, 810-821.

Garibaldi, L.A., Steffan-Dewenter, I., Kremen, C., Morales, J.M., Bommarco, R., Cunningham, S.A., Carvalheiro, L.G., Chacoff, N.P., Dudenhöffer, J.H., Greenleaf, S.S., Holzschuh, A., Isaacs, R., Krewenka, K., Mandelik, Y., Mayfield, M.M., Morandin, L.A., Potts, S.G., Ricketts, T.H.,

Szentgyörgyi, H., Viana, B.F., Westphal, C., Winfree, R., Klein, A.M., 2011. Stability of pollination services decreases with isolation from natural areas despite honey bee visits. Ecology Letters 14, 1062-1072.
Garratt, M.P.D., Breeze, T.D., Boreux, V., Fountain, M.T., McKerchar, M., Webber, S.M., Coston, D.J., Jenner, N., Dean, R., Westbury, D.B., Biesmeijer, J.C., Potts, S.G., 2016. Apple Pollination: Demand Depends on Variety and Supply Depends on Pollinator Identity. PLOS ONE 11, e0153889.
Garratt, M.P.D., Coston, D.J., Truslove, C.L., Lappage, M.G., Polce, C., Dean, R., Biesmeijer, J.C., Potts, S.G., 2014. The identity of crop pollinators helps target conservation for improved ecosystem services. Biol. Conserv. 169, 128-135.
Haenke, S., Kovács-Hostyánszki, A., Fründ, J., Batáry, P., Jauker, B., Tscharntke, T., Holzschuh, A., 2014. Landscape configuration of crops and hedgerows drives local syrphid fly abundance. Journal of Applied Ecology 51, 505-513.
Hanley, M., Wilkins, J., 2015. On the verge? Preferential use of road-facing hedgerow margins by bumblebees in agro-ecosystems. Journal of Insect Conservation 19, 67-74.
Hannon, L.E., Sisk, T.D., 2009. Hedgerows in an agri-natural landscape: Potential habitat value for native bees. Biological Conservation 142, 2140-2154.
Kennedy, C.M., Lonsdorf, E., Neel, M.C., Williams, N.M., Ricketts, T.H., Winfree, R., Bommarco, R., Brittain, C., Burley, A.L., Cariveau, D., Carvalheiro, L.G., Chacoff, N.P., Cunningham, S.A., Danforth, B.N., Dudenhoffer, J.H., Elle, E., Gaines, H.R., Garibaldi, L.A., Gratton, C., Holzschuh, A., Isaacs, R., Javorek, S.K., Jha, S., Klein, A.M., Krewenka, K., Mandelik, Y., Mayfield, M.M., Morandin, L., Neame, L.A., Otieno, M., Park, M., Potts, S.G., Rundlof, M., Saez, A., Steffan-Dewenter, I., Taki, H., Viana, B.F., Westphal, C., Wilson, J.K., Greenleaf, S.S., Kremen, C., 2013. A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. Ecology Letters 16, 584-599.
Kleijn, D., Rundlöf, M., Scheper, J., Smith, H.G., Tscharntke, T., 2011. Does conservation on farmland contribute to halting the biodiversity decline? Trends in Ecology & Evolution 26, 474-481.
Kleijn, D., Winfree, R., Bartomeus, I., Carvalheiro, L.G., Henry, M., Isaacs, R., Klein, A.-M., Kremen, C., M'Gonigle, L.K., Rader, R., Ricketts, T.H., Williams, N.M., Lee Adamson, N., Ascher, J.S., Baldi, A., Batary, P., Benjamin, F., Biesmeijer, J.C., Blitzer, E.J., Bommarco, R., Brand, M.R., Bretagnolle, V., Button, L., Cariveau, D.P., Chifflet, R., Colville, J.F., Danforth, B.N., Elle, E., Garratt, M.P.D., Herzog, F., Holzschuh, A., Howlett, B.G., Jauker, F., Jha, S., Knop, E., Krewenka, K.M., Le Feon, V., Mandelik, Y., May, E.A., Park, M.G., Pisanty, G., Reemer, M., Riedinger, V., Rollin, O., Rundlof, M., Sardinas, H.S., Scheper, J., Sciligo, A.R., Smith, H.G., Steffan-Dewenter, I., Thorp, R., Tscharntke, T., Verhulst, J., Viana, B.F., Vaissiere, B.E., Veldtman, R., Westphal, C., Potts, S.G., 2015. Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. Nat Commun 6.
Kromp, B., 1999. Carabid beetles in sustainable agriculture: a review on pest control efficacy, cultivation impacts and enhancement. Agriculture, Ecosystems & Environment 74, 187-228.
Lacoeuilhe, A., Machon, N., Julien, J.F., Kerbiriou, C., 2016. Effects of hedgerows on bats and bush crickets at different spatial scales. Acta Oecologica-International Journal of Ecology 71, 61-72.
Lang, A., 2003. Intraguild interference and biocontrol effects of generalist predators in a winter wheat field. Oecologia 134, 144-153.
Larsson, H., 2005. A crop loss model and economic thresholds for the grain aphid, Sitobion avenae (F.), in winter wheat in southern Sweden. Crop Protection 24, 397-405.
Losey, J.E., Vaughan, M., 2006. The Economic Value of Ecological Services Provided by Insects. Bioscience 56, 311-323.
Macfadyen, S., Muller, W., 2013. Edges in Agricultural Landscapes: Species Interactions and Movement of Natural Enemies. PloS one 8, e59659.

Matson, P.A., Parton, W.J., Power, A.G., Swift, M.J., 1997. Agricultural intensification and ecosystem properties. Science 277, 504-509.
Maudsley, M.J., 2000. A review of the ecology and conservation of hedgerow invertebrates in Britain. Journal of Environmental Management 60, 65-76.
Mitchell, M., Bennett, E., Gonzalez, A., 2013. Linking landscape connectivity and ecosystem service provision: current knowledge and research gaps. 16, 894-908.
Morandin, L.A., Kremen, C., 2013. Hedgerow restoration promotes pollinator populations and exports native bees to adjacent fields. Ecol. Appl. 23, 829-839.
Morandin, L.A., Long, R.F., Kremen, C., 2014. Hedgerows enhance beneficial insects on adjacent tomato fields in an intensive agricultural landscape. Agriculture, Ecosystems & Environment 189, 164-170.
Morandin, L.A., Long, R.F., Kremen, C., 2016. Pest Control and Pollination Cost–Benefit Analysis of Hedgerow Restoration in a Simplified Agricultural Landscape. Journal of Economic Entomology 109, 1020-1027.
Natural England, 2013. Entry Level Stewardship Environmental Stewardship Handbook, Fourth Edition - January 2013.
Natural England, 2014. Priority Habitat Inventory (England). Open Government Licence.
Norton, L.R., Maskell, L.C., Smart, S.S., Dunbar, M.J., Emmett, B.A., Carey, P.D., Williams, P., Crowe, A., Chandler, K., Scott, W.A., Wood, C.M., 2012. Measuring stock and change in the GB countryside for policy – Key findings and developments from the Countryside Survey 2007 field survey. Journal of Environmental Management 113, 117-127.
Nyffeler, M., Sunderland, K.D., 2003. Composition, abundance and pest control potential of spider communities in agroecosystems: a comparison of European and US studies. Agriculture, Ecosystems & Environment 95, 579-612.
Ponisio, L.C., M'Gonigle, L.K., Kremen, C., 2016. On-farm habitat restoration counters biotic homogenization in intensively managed agriculture. Global Change Biology 22, 704-715.
Ramsden, M., Menendez, R., Leather, S., Wäckers, F., 2016. Do natural enemies really make a difference? Field scale impacts of parasitoid wasps and hoverfly larvae on cereal aphid populations. Agricultural and Forest Entomology, n/a-n/a.
Ramsden, M.W., Menéndez, R., Leather, S.R., Wäckers, F., 2015. Optimizing field margins for biocontrol services: The relative role of aphid abundance, annual floral resources, and overwinter habitat in enhancing aphid natural enemies. Agriculture, Ecosystems & Environment 199, 94-104.
Rusch, A., Bommarco, R., Jonsson, M., Smith, H.G., Ekbom, B., 2013. Flow and stability of natural pest control services depend on complexity and crop rotation at the landscape scale. Journal of Applied Ecology 50, 345-354.
Sardiñas, H.S., Kremen, C., 2015. Pollination services from field-scale agricultural diversification may be context-dependent. Agriculture, Ecosystems & Environment 207, 17-25.
Schmidt, M.H., Lauer, A., Purtauf, T., Thies, C., Schaefer, M., Tscharntke, T., 2003. Relative importance of predators and parasitoids for cereal aphid control. Proceedings of the Royal Society B: Biological Sciences 270, 1905-1909.
Shackelford, G., Steward, P.R., Benton, T.G., Kunin, W.E., Potts, S.G., Biesmeijer, J.C., Sait, S.M., 2013. Comparison of pollinators and natural enemies: a meta-analysis of landscape and local effects on abundance and richness in crops. Biological Reviews 88, 1002-1021.
Staley, J.T., Botham, M.S., Chapman, R.E., Amy, S.R., Heard, M.S., Hulmes, L., Savage, J., Pywell, R.F., 2016. Little and late: How reduced hedgerow cutting can benefit Lepidoptera. Agriculture Ecosystems & Environment 224, 22-28.
Staley, J.T., Bullock, J.M., Baldock, K.C.R., Redhead, J.W., Hooftman, D.A.P., Button, N., Pywell, R.F., 2013. Changes in hedgerow floral diversity over 70 years in an English rural landscape, and the impacts of management. Biological Conservation 167, 97-105.

Staley, J.T., Sparks, T.H., Croxton, P.J., Baldock, K.C.R., Heard, M.S., Hulmes, S., Hulmes, L., Peyton, J., Amy, S.R., Pywell, R.F., 2012. Long-term effects of hedgerow management policies on resource provision for wildlife. Biological Conservation 145, 24-29.
Sunderland, K., Samu, F., 2000. Effects of agricultural diversification on the abundance, distribution, and pest control potential of spiders: a review. Entomol. Exp. Appl. 95, 1-13.
Sunderland, K.D., Fraser, A.M., Dixon, A.F.G., 1986. Field and Laboratory Studies on Money Spiders (Linyphiidae) as Predators of Cereal Aphids. J. Appl. Ecol. 23, 433-447.
Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I., Thies, C., 2005. Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. Ecology Letters 8, 857-874.
Woodcock, B.A., Bullock, J.M., McCracken, M., Chapman, R.E., Ball, S.L., Edwards, M.E., Nowakowski, M., Pywell, R.F., 2016. Spill-over of pest control and pollination services into arable crops. Agriculture, Ecosystems & Environment 231, 15-23.
Zhang, W., Swinton, S.M., 2009. Incorporating natural enemies in an economic threshold for dynamically optimal pest management. Ecol. Model. 220, 1315-1324.

Table 1. Effects of hedgerow quality, % semi natural landscape within 500m and distance from the hedgerow on aphids, natural enemies and pollinators. Values for degrees of freedom, F and p following analysis with linear mixed effects models shown.

	Hedge Quality			% Semi-natural			Distance			% Semi-natural:distance		
	d.f.	F	P	d.f.	F	P	d.f.	F	P	d.f.	F	P
Total aphids	1,35	0.37	0.55	1,430	0.47	0.49	1,430	6.36	**0.012***			
M. dirhodum	1,35	0.23	0.63	1,430	0.00	0.98	1,430	6.79	**0.0095****			
S. avenae	1,35	0.49	0.49	1,430	2.63	0.11	1,430	3.26	0.072			
Carabids	1,22	0.63	0.44	1,22	0.11	0.74	1,287	1.14	0.29			
Staphylinids	1,22	1.15	0.30	1,22	0.15	0.70	1,286	4.85	**0.029***	1,286	4.11	**0.044***
Lycosids	1,22	4.10	**0.055.**	1,22	6.85	**0.016***	1,287	130.76	**<0.001*****			
Linyphiids	1,22	4.30	**0.049***	1,22	0.60	0.45	1,287	9.50	**0.0023****			
Total bees	1,34	1.71	0.20	1,34	6.20	**0.018***	1,94	35.84	**<0.001****			
Honey bees	1,34	0.33	0.57	1,34	2.79	0.10						
Solitary bees	1,34	0.14	0.71	1,34	1.97	0.17						
Hoverfly	1,34	0.058	0.81	1,34	2.45	0.13	1,94	16.11	**<0.001*****			
Bombus sp.	1,34	5.28	**0.028***	1,34	2.75	0.11						

Fig. 1. Sixteen study sites across four landscape blocks in south eastern England (a). Within each landscape block four hedgerows next to winter wheat fields were studied (b) with two hedgerows of good quality (1, 2) and two of poor quality (3, 4) in each block. Hedgerows 1 & 3 were located in areas of high semi-natural habitat (Area shown in green) while 2 & 4 were in low semi-natural areas.

Figure 2. Natural enemy abundance in wheat fields in relation to a) distance from hedgerows and b) surrounding area of semi-natural habitat within a 500m radius. Data shows log +1 abundance per sampling point. Analysis with linear mixed effects models with taxa showing a significant response ($p < 0.05$) marked with an asterisk. Grey area shows 95% confidence interval.

Figure 3. Aphid abundance in wheat fields in relation to a) distance from hedgerows and b) surrounding area of semi-natural habitat within a 500m radius. Data shows log +1 abundance per sampling point. Analysis with linear mixed effects models with taxa showing a significant response ($p < 0.05$) marked with an asterisk. Grey area shows 95% confidence interval.

Figure 4. Pollinator abundance in wheat fields in relation to a) distance from hedgerows and b) surrounding area of semi-natural habitat within a 500m radius. Data shows log +1 abundance per sampling point. Analysis with linear mixed effects models with taxa showing a significant response ($p < 0.05$) marked with an asterisk. Grey area shows 95% confidence interval.

Figure 1

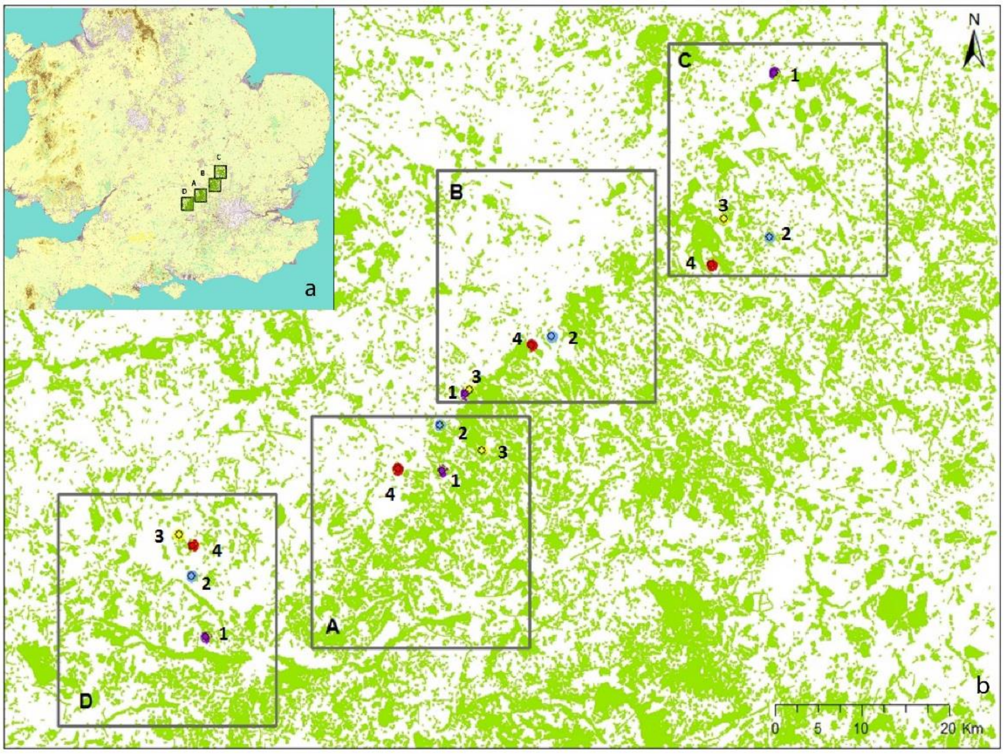

Figure 2

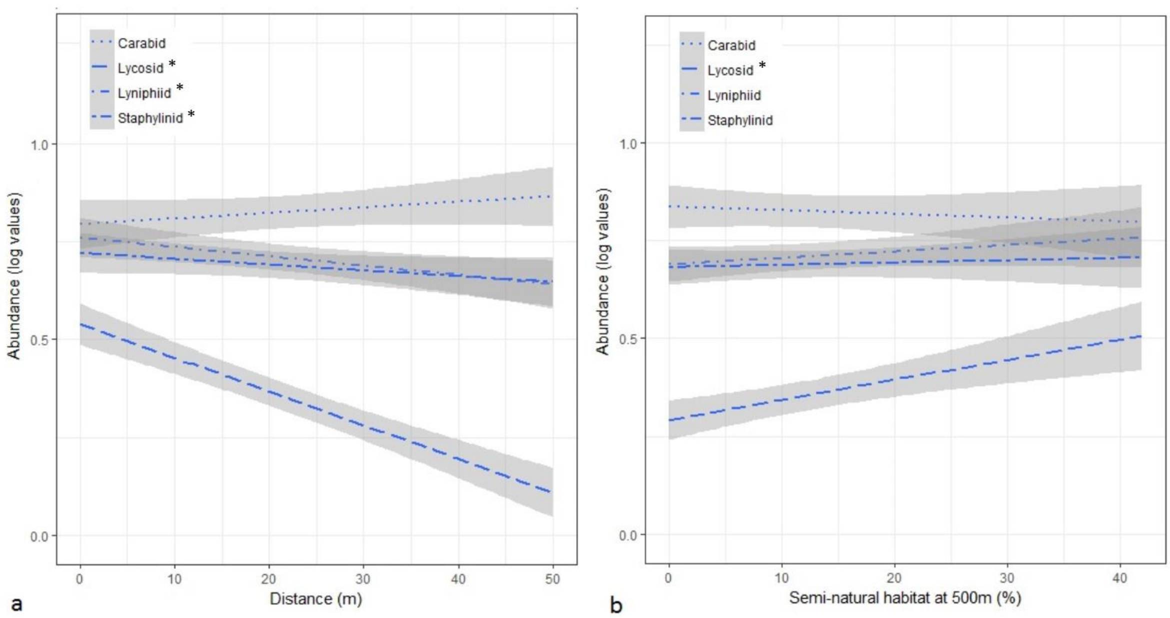

Figure 3

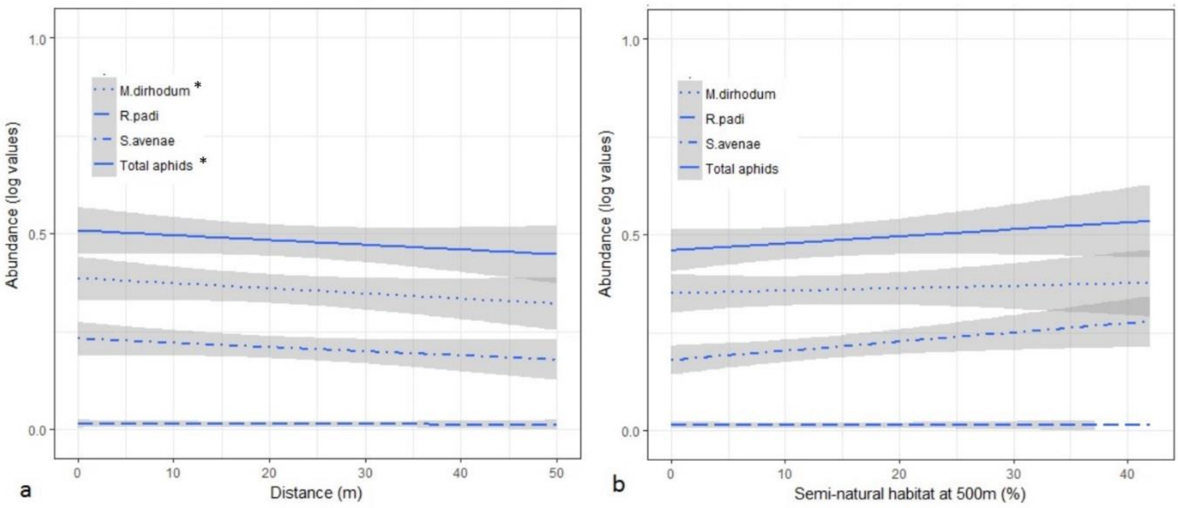

Figure 4