

Impacts of mixed farming systems on nocturnal invertebrates and bats

Rochelle Kennedy

September 2025

Thesis submitted for the degree of
Doctor of Philosophy
Biological & Environmental Sciences, School of Natural
Sciences
The University of Stirling

Summary

Intensive farming is a key driver of insect declines across the globe, via homogenisation of landscapes, use of synthetic fertilisers and insecticides, land use change and habitat loss. Declining insect abundance may have bottom-up effects on insectivores such as bats. Mixed farming, where crops and livestock are integrated into the crop rotation is thought to mitigate biodiversity declines via reduced synthetic inputs and increasing landscape heterogeneity. In addition, mixed farming could be beneficial for bats in the autumn, as pasture or livestock may provide greater insect resources than bare (i.e. harvested) arable fields at a time of year that is crucial for bats feeding up prior to hibernation. In chapters two to four I aimed to assess the direct and indirect effects (mediated by landscape attributes and local features) on bats and nocturnal insects. I collected data across 26 farms in North-East Scotland (13 mixed and 13 arable farms) on nocturnal insect abundance and diversity using light trapping during the summer months and bat activity during both the summer months and the autumn using acoustic methods. I found very little overall benefit of mixed compared with arable farming. Key findings were that *Pipistrelle* habitat selection was different between the two farm types, with *Pipistrellus pygmaeus* avoiding arable fields and selecting woodland where this was available. *Pipistrellus pipistrellus* preferred buildings on both farm types and avoided arable fields on mixed farms in favour of pasture. In addition, woodland edge density at the landscape scale, which was slightly higher on mixed farms, was positively associated with bat activity, moth abundance and moth species richness. Taller hedgerows, which were marginally lower on mixed farms benefitted both bats and a range of insect groups. Insect abundance and diversity and bat activity were similar over pasture than between crop fields, suggesting that pasture management may be preventing mixed farming from being beneficial. Thus, in chapter five I assessed the effect of a regenerative grazing practice, 'mob-grazing' on moths. Mob grazing aims to mimic wild

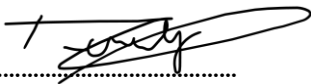
megaherbivore grazing behaviour by increasing herd size whilst also increasing pasture rest time and moving livestock daily. I compared moth abundance and diversity in 13 fields mob grazed by cattle and 13 set-stock fields (where cattle are kept in the same field for several weeks). I found no direct benefit of mob grazing on moths. However, mob grazing reduced the negative effect of sheep grazing on caterpillar abundance. Grazing intensity also had a negative effect on caterpillar abundance and species richness. Findings from this thesis can help to inform both farmers seeking to mitigate biodiversity loss and government agricultural policies that aim to encourage wildlife-friendly farming practices.

Ethical approval

Ethical approval was granted by AWERB for all data collection carried out as part of this thesis. Data collection for chapters two, three and four were all granted ethical approval under both the reference numbers AWERB 2022 7480 6478 and AWERB 2023 13544 9047. Ethical approval for data collected in chapter five was granted under reference numbers GUEP 2023 13606 9048 and AWERB 2023 13544 9047.

Declaration

I hereby declare that this thesis has been composed by myself and that it embodies the results of my own research. Where appropriate, I have acknowledged the nature and extent of work carried out in collaboration with others. Artificial intelligence software was not used for data generation or in any part of writing of this thesis. I consent to the use of plagiarism detection software.



.....

Rochelle Kennedy

Acknowledgements

This thesis would never have come together had it not been for the best team of supervisors that a PhD student could ask for. Kirsty, thank you so much for helping me to think outside the box whenever I was stuck on something. Elisa, you never failed to provide valuable knowledge and advice on everything from bats to stats. Thank you to Nick, for being an amazing mentor and always being willing to help out with anything, even if it meant getting stuck in a bog on a farm in the middle of the night with a bat detector! I also owe a huge thanks to Charlotte Wood, for dedicating countless hours of her time to assist me with fieldwork. Whether it was trudging around a farmer's field in the dead of night with a bat detector, or painstakingly searching for caterpillars, Charlotte – you always had a smile and were well prepared with a suitable playlist for our long car journeys together across Scotland. Many thanks also go to all of the other students who gave up their time to search for caterpillars on cold spring nights (Vanessa Conjar, Trudi Hayes, Clare Stewart, Emma Hathaway and Heather Lawson). Thank you to all those who provided valuable advice throughout my PhD. To David Hood for taking the time to show me how to construct a home-made moth trap. To Patrick Cook for all of the time you gave me to chat about surveying for caterpillars, and to Mark Young for putting up with my 'battered' moth samples and helping with identification of all of my tiny brown micro moths. This project would obviously have not been possible without the close cooperation of the many farmers and landowners who granted permission for me to undertake surveys on their land. I am very grateful for all of the time that you gave me and for the occasional free ride on a quad bike over bumpy fields! My fellow PhD students at SRUC have been an amazing support network throughout this journey and I will miss you all. Verena, you have been an amazing friend and office buddy, thank you for always being there when times got tough. Claire, the office would have been so lonely without you this last year, thank you for always being happy to listen to both my rants and jokes! I

am also very grateful to all of the members from my lab group at The University of Stirling for providing support and knowledge. In particular, to Emily for answering my endless Structural Equation Modelling questions and to Eleri for helping with anything bat related. Finally, a huge thank you to my husband Steve and daughter Bobbi for putting up with me being tired and grumpy sometimes after a long night in the field, for always being supportive and for moving to Scotland with me so that I could accomplish this journey. Finally, thank you to mum and dad for always being at the end of the phone when I needed it.

Table of Contents

Summary	2
Acknowledgements	5
List of figures	12
List of tables	14
List of supplementary material	15
Chapter 1. Introduction	18
1.1. From small-scale integrated farming to intensive agriculture	18
1.1.1. A brief history of agriculture	18
1.1.3. The industrial revolution and agricultural intensification.....	20
1.1.4. The influence of agricultural policies on the farming landscape in Europe	21
1.2. Impacts of widespread intensive farming on biodiversity	24
1.2.1. What is biodiversity?.....	24
1.2.2. Biodiversity status	25
1.2.3. Drivers of biodiversity decline	27
1.3. Benefits and short-fallings of current agricultural policies to protect biodiversity	29
1.3.1. Agri-environment schemes	29
1.4. Potential future solutions and gaps in knowledge	31
1.4.1. Regenerative farming.....	31
1.4.2. Mixed farming	32
1.5. Moths	33
1.5.1. Moth ecology	33
1.5.2. Conservation status of Lepidoptera	34
1.5.3. Threats to moths.....	35
1.6. Bats.....	37
1.6.1. Bat ecology.....	37
1.6.2. Conservation status of bats	39
1.6.2. Threats to bats	40
1.7. Thesis outline and aims	42
Chapter 2: Does mixed farming benefit moths? Exploring how different farming systems shape both local features and the wider landscape.....	43
Abstract	44

2.1. Introduction	45
2.2. Method	49
2.2.1. Site selection	49
2.2.2 Moth trapping	50
2.2.3. Landscape analysis	52
2.2.4. Local features.....	54
2.2.5. Statistical analysis.....	55
2.2.5.1. Metamodel specification	55
2.2.5.2. Mixed farm analysis: comparison of crop-crop and grass-crop margins.....	57
2.2.5.3. Community analysis	58
2.3. Results	60
2.3.1. Direct and indirect effect of farm type on moths	60
2.3.1.1. Landscape composition.....	60
2.3.1.2. Farm type	61
2.3.1.3. Local-scale features.....	62
2.3.2. Mixed farming: influence of pasture on moths	65
2.3.3. Moth community composition	65
2.3.3.1. Influence of landscape-scale features on community composition	65
2.3.3.2. Influence of local-scale features on community composition	66
2.4. Discussion.....	67
2.4.1. Farming strategies	67
2.4.2. Importance of landscape configuration for moths.....	69
2.4.3. Importance of local-scale woody features for moths.....	71
2.4.4. Conclusion	71
2.3. Acknowledgements	72
Chapter 3: Direct and indirect effects of mixed farming systems on nocturnal aerial invertebrates, mediated by local features and landscape attributes.....	95
Abstract	95
3.1. Introduction.....	96
3.2. Method.....	98
3.2.1. Site selection	98

3.2.2. Insect sampling	99
3.2.3. Data analysis	101
3.2.3.1. Landscape variable selection	101
3.2.3.2. Assessing direct and indirect effects of mixed farming	102
3.2.3.3. Assessing the importance livestock stocking rate and pasture presence	104
3.3. Results	105
3.3.1. Overview	105
3.3.2. Direct and indirect effects of farm type on aerial invertebrates mediated by local features and landscape attributes	106
3.2.3. Effects of pasture and livestock stocking rate on invertebrates	109
3.4. Discussion.....	112
3.4.1. Direct effects of farm type	113
3.4.2. Indirect effects of mixed farming mediated by landscape attributes.....	113
3.4.3. Importance of local woody features	115
3.4.4. Livestock management on mixed farms	115
3.4.5. Management recommendations	116
Acknowledgements.....	117
Chapter 4: Contrasting effects of mixed farming on bats are mediated by local and landscape features and differ between seasons	129
Abstract.....	129
4.1. Introduction.....	130
4.2. Methods.....	132
4.2.1. Site selection	132
4.2.2. Bat surveys	133
4.2.2.1. Walked transects.....	133
4.2.2.2. Static detectors	134
4.2.3. Acoustic analysis	136
4.2.4. Habitat analysis of transects	137
4.2.5. Landscape analysis.....	138
4.2.6. Statistical analysis	139
4.2.6.1. Habitat preference on mixed and arable farms.....	139
4.2.6.2. Structural equation modelling: exploring direct and indirect effects of farm type	139

4.2.6.3. Effects of pasture presence and management on mixed farms	142
4.3. Results	143
4.3.1. Habitat preferences of foraging bats in mixed and arable farms.....	143
4.3.2. Effects of mixed farming, landscape and local attributes on bats	145
4.3.3. Effects of pasture presence and livestock management	148
4.4. Discussion.....	150
4.4.1. Bat habitat preferences differ between mixed and arable farms	150
4.4.2. Importance of landscape composition and configuration	151
4.4.3. Importance of local woody features	153
4.4.4. Stocking rate is more important than pasture presence for bat activity on mixed farms.....	154
4.4.5. Management recommendations	154
Acknowledgements.....	155

Chapter 5: Impacts of regenerative agriculture on biodiversity: does ‘mob- grazing’ benefit moths? 170

Abstract.....	170
5.1. Introduction.....	171
5.2. Methods	174
5.2.1. Site selection	174
5.2.2. Surveying moth larvae	176
5.2.3. Sweep netting.....	177
5.2.4. Manual searches	177
5.2.5. Species identification	178
5.2.6. Surveying adult moths	178
5.2.7. Plant surveys	179
5.2.8. Data analysis	180
5.3. Results	181
5.3.1. Overview	181
5.3.2. Effects of livestock grazing management on Lepidoptera	182
5.3.3. Effects of pasture composition.....	184
5.4. Discussion.....	186
5.4.1. Mob grazing and livestock management	186
5.4.2. Pasture composition	188

5.4.3. Management recommendations	188
Acknowledgements.....	189
Chapter 6: Discussion	198
6.1. Is mixed farming beneficial for bats and nocturnal insects overall?	199
6.1.1. A mismatch of scales.....	199
6.1.2. Overall effects of mixed farming.....	202
6.2. Importance of landscape attributes for different taxonomic groups	204
6.3. Importance of linear woody features for different taxonomic groups....	207
6.4. Effects of stocking rate on mixed farms.....	210
6.5. Benefits of a regenerative grazing practice: mob-grazing.....	211
6.6. The context of future agricultural policies and trends in farming.....	212
6.7. Complementarity and limitations of survey methods for bats and nocturnal invertebrates	215
6.7.1. Bats	215
6.7.2. Moths	217
6.8. Management recommendations	218
References	220

List of figures

Chapter one

Figure 1.1. Mural located in the burial chamber of Sennedjem in Theben, Egypt.....	19
Figure 1.2: Change in agricultural land cover preceding, during and after the industrial revolution.....	21
Figure 1.3 Change in area cover and abundance of mixed crop–livestock systems since 1975 globally and in Europe.....	23
Figure 1.4. Path diagram showing potential direct and indirect benefits of integrating livestock on bats and their insect prey.....	33

Chapter two

Figure 2.1. Conceptual model.....	49
Figure 2.2. Example locations of moth traps placed on both studied farm systems.....	51
Figure 2.3. Metamodel showing all variables and pathways that were included in SEMs.....	57
Figure 2.4. Abundance and species richness of macro and micro moths by functional group.....	60
Figure 2.5. Path diagrams for all SEMs where variables of interest had a significant effect on moths.....	63
Figure 2.6. Boxplots showing differences in moth abundance, species richness and diversity between crop-crop and grass-crop margins on mixed farms.....	64
Figure 2.7. NMDS plots of moth community composition at the farm scale and at the local scale.....	66

Chapter three

Fig 3.1. Set-up of insect traps.....100

Figure 3.2. Boxplots showing abundance and diversity of aerial insects in traps
.....106

Fig 3.3. SEM path diagrams for nocturnal aerial invertebrates.....109

Figure 3.4: Boxplots showing abundance and diversity of aerial insects in traps
placed in crop-crop margins and traps placed in crop-pasture margins.....112

Chapter four

Figure 4.1. Set-up of static detectors and example of transect route
design.....136

Figure 4.2. Metamodel showing hypothesized pathways between
variables.....142

Figure 4.3. Habitat selection of *P. pipistrellus* and *P. pygmaeus* on arable and
mixed farms.....144

Figure 4.4. SEM path diagrams for *P. pipistrellus*, *P. pygmaeus* and *Myotis* spp.
for summer and autumn.....147

Figure 4.5. Predicted change in *P. pipistrellus* and *P. pygmaeus* activity and
Myotis occurrence with cattle stocking rate.....149

Chapter 5

Figure 5.1. Map showing location of the study area within the UK and
approximate location of farm pairs.....176

Figure 5.2. Experimental set up of transects and quadrats within a
field.....178

Figure 5.3. Boxplots showing the interaction between grazing treatment and the
presence of sheep grazing on larval abundance and larval species richness and

scatterplots showing the effect of grazing intensity on larval abundance, larval species richness and adult moth abundance.....	183
---	-----

Chapter 6

Fig 6.1. Summary of the effect of woody feature height across different taxonomic groups.....	202
---	-----

Figure 6.2. Infographic summarising results across all structural equation models.....	209
--	-----

List of tables

Chapter 1

Table 1.1. Summary of changes to agricultural landscapes and practices in the UK over the past century.....	24
---	----

Chapter 3

Table 3.1: GLMM output summary table for the effects of pasture and livestock stocking rate on aerial invertebrates.....	111
--	-----

Chapter 5.

Table 5.1. Summaries for averaged models.....	185
---	-----

Chapter 6

Table 6.1. Average field rates (2018 – 2022) of total nitrogen (kg/Ha) applications in Great Britain on different crops and improved grassland ^a	207
---	-----

List of supplementary material

Chapter 2:

Figure S.2.1: Structural equation models where there was neither a direct or indirect effect of mixed farming on moths.....	73
Table S.2.1. Table of crop categories used for calculating crop diversity index.....	74
Figure S.2.2. NMDS ordination plots of dissimilarities between moth communities at the farm and trap level.....	75
Table S.2.2. Pearson correlation matrix of all variables considered for statistical analysis.....	76
Figure S.2.3. Boxplots showing differences in presence-absence of the 10 most common woody plant species with varying woody feature height.....	77
Table S.2.3. R squared values and pseudo r squared values that were used for landscape variable selection.....	78
Table S.2.4.: Summary of synthetic nitrogen fertiliser applications for the year of 2022 for mixed and arable farms used in this study.....	79
Table S.2.5: Model estimates for all pathways and correlated errors included in all moth SEMs.....	79
Table S.2.6. Species scientific names, abbreviations used in NMDS plots and total number of individuals per species.....	88
Table S.2.7. Summary table for GLMMs comparing moth abundance, species richness and diversity in crop-crop margins and crop-grass margins on mixed farms.....	93
Table S.2.8.1. PERMANOVA summary table for farm-level analysis of moth community composition.....	94

Table S.2.8.2: PERMANOVA summary table for trap-level analysis of moth community composition.....	94
---	----

Chapter 3:

Figure S.3.1. Map showing a. location of study area and b. approximate locations of study sites.....	118
--	-----

Figure S.3.2. R ² values obtained for different landscapes metrics at different scales.....	119
--	-----

Table S.3.1. Reclassification of habitat types from land cover maps into biotypes.....	120
--	-----

Table S.3.2. Grouping of crops into functional groups.....	120
--	-----

Tables S.3.3. Correlation matrix of landscape variables.....	121
--	-----

Table S.3.4. Full SEM results for nocturnal aerial invertebrates.....	123
---	-----

Figure S.3.3. Boxplots of insect abundance or diversity on farms with sheep grazing and without sheep grazing.....	127
--	-----

Figure S.3.4. Scatterplot of insect abundance at increasing stocking rates of cattle.....	128
---	-----

Chapter 4

Figure S.4.1: Map showing a. location of study area and b. approximate locations of study sites.....	156
--	-----

Table S.4.1. Settings used to configure Audiomoths.....	156
---	-----

Figure S.4.2. Plots showing the relationship between a. <i>P. pygmaeus</i> activity and feeding buzzes and b. <i>P. pipistrellus</i> activity and feeding buzzes.....	157
---	-----

Table S.4.2: Kaleidoscope settings.....	157
---	-----

Figure S.4.3: plots showing r^2 values for each landscape variable across different scales and between season for <i>P. pipistrellus</i> , <i>P. pygmaeus</i> and <i>Myotis</i> spp.....	158
Table S.4.3: CEH landcover map habitats re-classified.....	159
Figure S.4.4: boxplots showing the number of Pipistrelle passes on mixed farms associated with crop-crop and grass-crop margins across the two seasons.....	160
Table S.4.4. Correlation matrix for landscape and local variables.....	161
Table S.4.5. Observed and expected number of Pipistrelle passes on arable farms.....	164
Table S.4.6: Full SEM results for bats including correlated errors.....	165
Table S.4.7: GLMM results for the effect of stocking rate and margin type on bat activity on mixed farms.....	169

Chapter 5

Figure S.5.1. Boxplots showing the differences between mob-grazed and set-stocked for measures of vegetation characteristics and cattle stocking management.....	190
Table S.5.2. Abundances of all species found during larval surveys, with detailed information on family, overwintering strategy and guild classification.....	191
Table S.5.3. Adult moth species recorded during light trapping.....	192
Table S.5.4. Frequency of occurrence in quadrats of all plant species (or aggregate groups) recorded.....	193
Table S.5.5. r^2 values for measures of vegetation composition.....	195
Table S.5.6. Model summaries for all models included in model averaging and full models.....	196

Chapter 1. Introduction

1.1. From small-scale integrated farming to intensive agriculture

1.1.1. A brief history of agriculture

The exact origin of agriculture is a topic of hot debate but is thought to have been initiated by the domestication of wild wheat, which likely took place across multiple regions somewhere during the Neolithic period between 9,500 and 10,500 years ago (Fuller et al., 2011; Tanno and Willcox, 2006). The widespread domestication of livestock is thought to have occurred at a similar time (Noda et al., 2018; Zeder and Hesse, 2000) and likely contributed to the change from hunter-gatherers to Neolithic farming. Domestic cattle were initially herded for meat (Arbuckle et al., 2016), however their role in crop cultivation developed with the appearance of the first ox-drawn ploughs (Boggard, 2004). The invention of various forms of plough allowed cultivation of larger areas and soils that were previously difficult to cultivate. Agriculture expanded and the production of surplus food became possible. This new-found food security facilitated population increase and the rise of some of the most successful civilisations notably in China, Egypt and Mesoamerica (Chu and Xu, 2024; Figure. 1.1). With this agricultural expansion, woodlands were progressively cleared across Europe (Fyfe et al., 2015), likely to create space for crop fields and pasture. Strips of trees were left in place to delineate fields, as barriers for livestock and as a source of wood fuel (Forman and Baudry, 1984). Over time these strips of trees were colonised by other plants and resembled the hedgerow system that we see today in Western Europe (Baudry et al., 2000). By 1000 BCE the majority of woodland clearance had already taken place in Europe and woodland cover was similar to that at the start of the industrial revolution (Fyfe et al., 2015). Evidence of the gradual degradation of forests in East Asia, driven by agricultural practices, also occurred during a similar time period (Zhou et al., 2023).

Towards the mid to end of the Neolithic period, livestock played an increasingly important role in agriculture, with evidence that livestock manure was added to fields as early as 5950 BCE in Greece (Vaiglova et al., 2014). As far back as 6400 BCE there is evidence of crop rotations occurring in Europe, with several varieties of cereal grown and as well as several different crop types (Sabanov et al., 2024). Thus, farming systems at this time were highly diverse. Livestock were further integrated into crop farming from about 800 AD, through the rotation of pasture with crops and grazing of harvested crop fields with domestic livestock, otherwise called 'mixed farming' (Hamerow et al., 2019). Organic nutrient input from grazing livestock and spreading of manure can increase productivity of crops (Domingo-Olivé et al., 2016). This change in farming practices led to rapid expansion of cereal growing and a period which has been called the 'medieval agricultural revolution' (Hamerow et al., 2019). However, the most rapid change in agricultural practices was arguably initiated by the industrial revolution.



Figure 1.1. Mural located in the burial chamber of Sennedjem in Theben, Egypt, dating back to circa 1200 BCE, showing the role of livestock at the end of the Neolithic period. Photograph taken by (The Yorck Project, 2002) CC licence.

1.1.3. The industrial revolution and agricultural intensification

From the late Neolithic period until the industrial revolution agricultural practices in Europe remained largely the same. Mixed farming, where livestock are integrated into the crop rotation was widespread (Garrett et al., 2020; Sylvester and Cunfer, 2008). Crop rotation also likely included a fallow year (where no crops are grown) to reduce the persistence of crop pests and increase soil fertility, with some rotations also including a season of nitrogen-fixing legumes to further increase soil fertility (de Molina et al., 2015). However, starting in the 18th century in Europe, the industrial revolution sparked a rapid change in agricultural practices. Discovery of large fossil fuel reserves enabled the invention of coal-powered farming machinery, which would soon be replaced by oil-powered machinery. Crop fields that had until then been sown, harvested and ploughed with horse-drawn equipment could now be managed on a large scale with ease, which saw a further increase to the area dedicated to agricultural production in some parts of the world (Figure.1.2.). Steamships fuelled by coal appeared during the early 19th century and made the exchange of food across oceans feasible, motivating farmers to produce a greater quantity of product for the global market (O'Rourke, 1997). High energy fuels also enabled the production of synthetic fertilisers via the Haber-Bosch process, where atmospheric nitrogen (N_2) is combined with hydrogen (H_2) to create ammonia (NH_3) under high temperature and pressure. The appearance of cheap synthetic fertilisers reduced farmer's reliance on livestock for natural fertiliser and is one of the main drivers of the separation of crop-livestock or mixed systems, with most farmers beginning to specialise in either crop or livestock production after the second world war (Garrett et al., 2020). The rapid increase in mechanisation and the loss of traditional farming knowledge led to over-exploitation of the land, leading to environmental disasters in some parts of the world, such as extreme soil erosion during an extended period of drought in North American and Canadian prairies, between 1930 and 1940,

otherwise known as the great dust bowl (Lee and Gill, 2015) and similar dust storms and desertification in China that continue to present day (Zucca et al., 2022). In Europe, mediterranean regions are at high risk of desertification from agricultural practices (Salvati et al., 2016).

Agricultural area over the long-term, 1700 to 1964

Total areal land use for agriculture, measured as the combination of land for arable farming (cropland) and grazing in hectares.

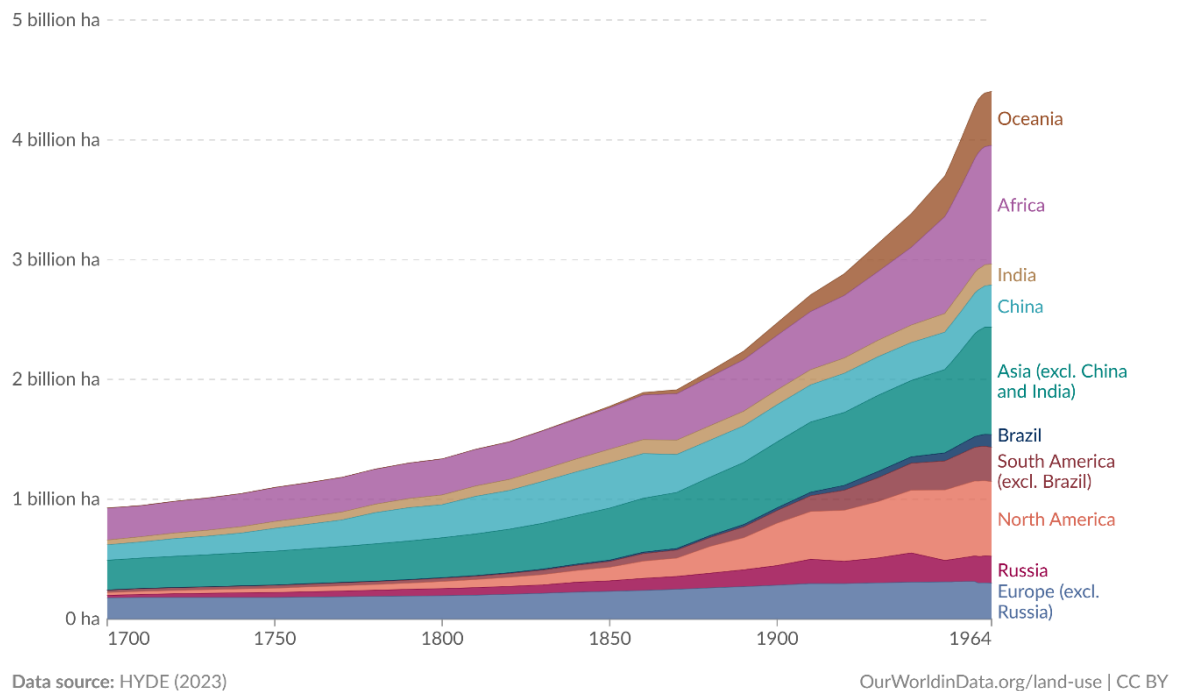


Figure 1.2: Change in agricultural land cover from 1700 to 1964 (HYDE, 2023).

1.1.4. The influence of agricultural policies on the farming landscape in Europe

After the second world war, the Common Agricultural Policy (CAP) was established in 1957 and financially encouraged a move towards self-sufficiency for countries belonging to the European Union. This sparked a huge increase in production and in England 41% of semi-natural grasslands were converted to improved pasture or arable between 1960 and 2013 (Ridding et al., 2015) with similar losses seen in other parts of Europe (Aune et al., 2018; Cousins and Eriksson, 2008). Semi-natural grasslands are grassland where there has been

little to no historic input of synthetic fertilisers and are characterised by a high proportion of native grass and forb species, whilst improved grasslands have often been re-seeded, receive regular applications of synthetic fertilisers and are thus characterised by a high proportion of *lolium* spp. (Jefferson et al., 2019).

Furthermore, by encouraging increasing productivity, the CAP incentivised the removal of hedgerows and many remaining patches of semi-natural habitat and an increase in field size. Semi-natural habitat is habitat that has been modified by humans but is still intact enough to harbour higher numbers of native plant species than moderately or heavily modified habitat. The classification of a particular habitat as 'semi-natural' can be subjective, but previous studies have used this term to describe broadleaf woodland, scrub and low-input high diversity grassland or meadows (Aguilera et al., 2020; Fuentes-Montemayor et al., 2011a; Litovska et al., 2025). It is estimated that England lost over half of its hedgerows between 1940 and 1990 (Robinson and Sutherland, 2002), with similar figures seen for Belgium (Deckers et al., 2005). Field size was also increased in many European countries. For example, in Germany mean field size increased from 1.2 Ha to 12.2 Ha between 1953 and 2000 (Baessler and Klotz, 2006). In South-West England mean field size increased from 5.5 to 9.5 ha between 1945 and 1994.

The CAP incentivised production of just a small number of commodity crop types. At the same time, a wide range of pesticides and herbicides had become available and meant that rotation of multiple crops to reduce crop pests was no longer necessary, leading to a reduction in the diversity of crops grown on farms in Europe (Abson, 2019). In the USA, similar policies (the US Farm Bill), led to a rapid decrease in crop diversity between the 1960's and 2021 (Ye et al., 2024). Further changes to the CAP in 1990 saw a shift from supporting 'production' to supporting 'income'. This meant that farmers were incentivised to maximise profit and farm more efficiently, leading to a further increase in the use of synthetic fertilisers, herbicides and pesticides to

increase yields and reduce loss of crops to pests (Aspinall and Staiano, 2019). This increase in the use of synthetic fertiliser further drove separation of crop-livestock systems, resulting in a steady decline of mixed farming across Europe between the 1970's and early 2000's (Figure 1.3.), with similar policies causing the decline of mixed farming in the United States (US), Canada and New Zealand (Garrett et al., 2020). Though mixed farming has seen an increase in total area coverage in Brazil and Uruguay (Figure 1.3). In the UK, permanent pasture (pasture this is greater than five years old) declined from 7.4. million hectares to 6.2 million hectares between 1920 and 2021, whilst numbers of cattle have double during a similar time period (though have been decreasing since 1985 (Zayed and Loft, 2019). This de-coupling of crop-livestock systems, loss of crop diversity and semi-natural areas over time and widespread use of synthetic inputs have led to the homogenous agricultural landscape that we see in the western world today (Van Der Sluis et al., 2019; van Zanten et al., 2014, Table 1.1) and is widely referred to as 'intensive agriculture'.

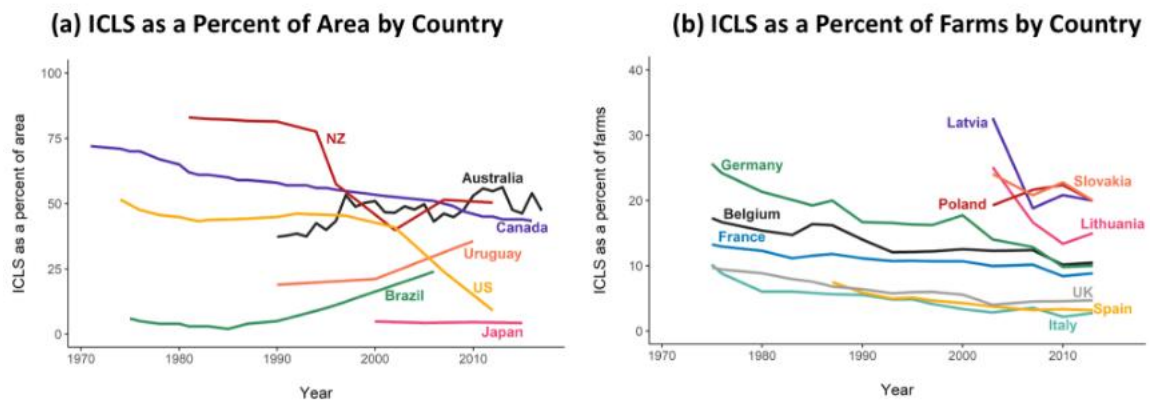


Figure 1.3: a. Change in the percentage of total area covered by integrated crop-livestock systems (ICLS) in countries across the world. b. Change in the percentage of farms practising integrated crop-livestock (ICLS) in countries in Europe (1975 – 2013). Figure from (Garrett et al., 2020)

Table 1.1. Summary of changes to agricultural landscapes and practices in the UK over the past century

	Location	Start value (and year)	End value (and year)	Source
Mean field size (ha)	South-west England	5.5 (1945)	9.5 (1994)	<i>(Robinson and Sutherland, 2002)</i>
	Cambridgeshire	6.5 (1945)	16 (1994)	
Estimated total hedgerow length (km)	UK	980 000 (1945)	390 000 (1994)	<i>(Robinson and Sutherland, 2002)</i>
Total area of permanent pasture (millions of ha)	UK	7.4 (1920)	6.2 (2021)	<i>(Zayed and Loft, 2019)</i>
Total cattle numbers (million)	UK	7.5 (1920)	44.5 (1990)	<i>(Zayed and Loft, 2019)</i>
Mean nitrogen application rate Kg N Ha ⁻¹	UK	32	125	<i>(Robinson and Sutherland, 2002)</i>

1.2. Impacts of widespread intensive farming on biodiversity

1.2.1. What is biodiversity?

Biodiversity is the variety of life in a given area and can be used to describe taxonomic diversity (the variety of species), functional diversity (the variety of roles that a species or group of species fulfil within a given ecosystem) or genetic diversity (the variety of genetic traits). High biodiversity makes an ecosystem robust to environmental change (McCann, 2000), with a reduction in species diversity associated with lower biomass production, nutrient cycling

and higher disease rate (Tilman et al., 2014). Current climate change trajectories predict severe increases in temperature, unpredictable precipitation patterns and an increase in the frequency and severity of extreme weather events (IPCC, 2023). Given the current and inevitable future pressure from climate change on agricultural systems, it is crucial to protect biodiversity if we are to preserve functioning agroecosystems over the coming decades.

1.2.2. Biodiversity status

There has been a rapid acceleration in species extinctions globally since the industrial revolution, with global extinction rates estimated to be at least ten to hundreds of times higher than the normal background rate (Humphreys et al., 2019; Proença and Pereira, 2013). Population decreases have been noted across a range of taxonomic groups and in a range of different locations. Insects have been particularly affected by population declines with around 25% of all species currently assessed by the International Union for Conservation of Nature (IUCN) undergoing significant population declines (IUCN, 2025). However, it is estimated that around 80% of invertebrate species are yet to be described and may already be under severe threat or already extinct (Stork, 2018). This means that in reality, only around 1 % of insect species have been assessed by the IUCN (IUCN, 2025).

Insect population trends in the UK are no different, with ground beetles having declined by at least 28% in a variety of habitat types (Brooks et al., 2012a). Long-term monitoring of aerial invertebrates shows that Diptera abundance has reduced by at least 37% between 1974 and 2014 at a monitoring location in Scotland (Grabener et al., 2020), with Diptera abundance reducing over a 30 year monitoring period in some parts of the UK but not others (Shortall et al., 2009). Native bees have seen population declines in both the UK

and the Netherlands, with parallel declines in their pollinated plants (Biesmeijer et al., 2006). Widespread and parallel declines in insectivorous birds and insect abundance have also been noted in Denmark in a 22 year study (Møller, 2019).

Terrestrial mammals are one of most well-studied taxonomic groups. Almost 30% of all assessed mammal species are currently considered near threatened, vulnerable, endangered or critically endangered by the IUCN red list. Of the 75 species of mammal with current threatened status in Europe, 25 are species of bat. In the UK, the last 50 years has seen a 7% decline in the abundance of mammals (Burns et al., 2023), with one in four mammals under threat of extinction in Britain (Mathews and Harrower, 2020).

Furthermore, long-term monitoring is relatively new and the loss of biodiversity that has occurred prior to these initiatives is largely unknown, though it is thought that biodiversity declines began before these monitoring programmes. For example, for plants, historic data is available and declining trends date back to at least 1930. In addition, the UK is estimated to have lost around 50% of its biodiversity based on Biodiversity Intactness Score (Burns et al., 2023) (where current abundance of species is compared with near-undisturbed sites).

These declines in biodiversity sparked 196 countries to sign an initial agreement in 1992 to reverse biodiversity declines. The Aichi targets set out clear targets to be achieved by 2020 by every participating country in order to protect and enhance biodiversity. However, none of the countries committed were able to achieve all targets, with the UK fairing particularly poorly, achieving only 5 of the 20 targets (JNCC, 2019). Following on from these failures, in 2022 a new international agreement was proposed: the Kunming–Montreal Global Biodiversity Framework (also referred to as the Biodiversity Plan for Life of Earth) which sets out goals for 2050. These new legally binding targets commit participating countries to halt decline in species populations by 2030 and increase biodiversity by 2050.

1.2.3. Drivers of biodiversity decline

The single biggest driver of terrestrial biodiversity decline is land-use change, but other important drivers exist including persecution and hunting, climate change and invasive species (Jaureguiberry et al., 2022). Whilst land-use change can be associated with urbanisation, it is most commonly driven by agriculture and more specifically, intensive agriculture. Intensive agriculture has been identified as one of the key drivers of population declines of a wide-range of taxonomic groups, including insects (Grevé et al., 2024; Potts et al., 2010), mammals (Brodie et al., 2021) and farmland birds (Reif and Hanzelka, 2020). These negative impacts can be tied to various aspects of intensive farming, that can act alone or interactively.

Synthetic fertiliser applications on crops favour competitive plant species in field margins (Schmitz et al., 2014). These nutrient-loving plant species can then out-compete slower growing species, leading to lower plant diversity (Liu et al., 2025), thus providing a lower diversity of plant food for phytophagous insects and less flowering plants for pollinators (Russo et al., 2023). Synthetic herbicides can also reduce the availability of arable weeds within crop fields and spray drift reduces flowering forbs along field margins with impacts on pollinators (Dupont et al., 2018; Schmitz et al., 2014). The negative impacts of insecticides on non-target invertebrates and insectivore predators has been widely documented. The appearance of DDT as an agricultural insecticide has had lethal effects on bats (Geluso et al., 1976) and even after its ban in the 1970's continues to be found in invertebrates, fish and birds (Cipro et al., 2013; Windsor et al., 2019). Since the use of Neonicotinoids in agriculture became widespread in the 1990's, many studies have documented their toxicity for invertebrates (Pisa et al., 2015a; Zhao et al., 2020) and potentially insect predators such as birds (Eng et al., 2019).

The loss of semi-natural habitat associated with intensive farming has been another driver of biodiversity decline. In intensively farmed landscapes,

semi-natural grasslands provide important food resources and habitat for pollinators (Ockinger and Smith, 2007), birds (Rosch et al., 2023) and bats (Ancillotto et al., 2023; Ewert et al., 2023). In fact, abundance and diversity of many species groups on farmland has been found to increase with increasing amounts of semi-natural habitat in the surrounding landscape (Fuentes-Montemayor et al., 2011a; Raderschall et al., 2021).

Intensively managed agricultural fields may act as barriers to species dispersal, particularly for species with limited dispersal ranges such as plants in remnant grassland patches (Lindgren and Cousins, 2017). Movement between patches of habitat appears less limited by the surrounding agricultural matrix for more mobile species groups like bats (Mendenhall et al., 2014) and less quality habitats such as hedgerows and roadside verges can act as stepping-stones between semi-natural patches (Öckinger and Smith, 2007).

Crop monocultures driven by intensive farming practices are associated with lower biodiversity and higher risk of insect pest outbreaks than landscapes with high crop diversity (Gbèblonoudo Dassou et al., 2023; Kheirodin et al., 2020; O'Rourke et al., 2011), though multiple studies have found that the benefit of diversifying crops is only effective if a certain amount of semi-natural areas are also provided. For example, in (Aguilera et al., 2020) crop diversity only increased carabid and pollinator diversity in landscapes where there was at least 11% semi-natural habitat, with similar results reported for farmland bird diversity (Frank et al., 2024). Furthermore, in (Tassoni et al., 2024) aerial insect species richness was only enhanced by crop diversity if a high proportion of semi-natural habitat (as measured by field border density of at least 500 m Ha⁻¹) was present. In this study, semi-natural also interacted with grassland proportion, with a high proportion of field border density leading to a positive effect of the proportion of grassland on insect richness.

Thus, the removal of semi-natural areas associated with intensive agriculture not only has a direct impact on biodiversity through habitat loss

and reduced connectivity but also seems to reduce (or even reverse) the potential benefits of increasing crop diversity that is often associated with less intensive farming practices.

However, not all species are negatively affected by intensive farming. Many generalist species (characterised by their flexible diet and ability to thrive in a variety of habitat conditions) are able to benefit from anthropogenic environments and are increasing in abundance (Benmazouz et al., 2021; Fox et al., 2021). However, this increase in the abundance of generalists or opportunists often leads to homogenisation of communities and loss of functional diversity (Börschig et al., 2013), with implications for ecosystem services. Indeed, loss of diversity on farmland is associated with greater outbreaks of insect pests and consequential damage to crops (Gurr et al., 2003; Wilby and Thomas, 2002).

1.3. Benefits and short-fallings of current agricultural policies to protect biodiversity

1.3.1. Agri-environment schemes

In the face of biodiversity decline, policies have been put in place across the globe to encourage farmers to implement wildlife-friendly farming practices, though the majority of these policies are concentrated in countries with a higher level of economic development (Wuepper et al., 2024). In Europe, these policies have taken the form of Agri-Environment Schemes (AES), though similar schemes exist in the USA (the US Farm Bill). AES are government-ran schemes remunerating farmers to put in place certain actions on their land that are designed to benefit wildlife or improve ecosystem function. Schemes are often aimed at promoting certain species or species groups, for example: species-rich grassland for pollinators, beetle banks and conservation headlands for breeding birds. However, schemes can sometimes have benefits

for non-target taxa (Hof and Bright, 2010). Agri-environment schemes have been in place in Europe since 1985 and their effectiveness has been widely studied across different taxonomic groups. Management options such as buffer strips or grass margins have been found to benefit breeding birds and their insect prey (Josefsson et al., 2013), as well as queen bumblebees (Lye et al., 2009) and moths (Fuentes-Montemayor et al., 2011a). Reduced trimming of hedgerows under these schemes can increase species richness of bats (Froidevaux et al., 2019) and birds (Burgess et al., 2015). Organic farming (where synthetic inputs are not allowed) is also supported by these schemes in the UK and Europe. Whilst organic farming can benefit a variety of taxonomic groups (Inclán et al., 2015; Wickramasinghe et al., 2004), it is currently only implemented on about 3 % of all agricultural land in the UK (UK Government, 2025) so is unlikely to have a widespread impact on biodiversity unless uptake increases.

Whilst there are some AES success stories, there are also many species that have seen no benefit of AES. For example, the schemes studied in (Fuentes-Montemayor et al., 2011b) were of no benefit to Pipistrelle bats. In fact, higher bat activity and prey abundance was recorded on conventional farms that were not implementing AES. Similarly, organic farming on vineyards, implemented as an AES has no effect on bats, which responded only to landscape attributes (Froidevaux et al., 2017). In addition, there has been criticism that the outcomes of these schemes have gone unmonitored (Berendse et al., 2004) and even where long-term monitoring was put in place, few differences were found for the abundance of focal species in AES and non-AES managed features (MacDonald et al., 2019)

Some studies that have found benefits of AES have also noted an interaction of the effectiveness of AES with the surrounding landscape. For example, AES is most effective at increasing the species richness of birds, vascular plants and invertebrates at intermediate levels of landscape complexity (Concepción et al., 2012). In addition, other schemes are only

effective at increasing beetle abundance and species richness in areas of extensively managed farmland (Caro et al., 2016). Whilst the effectiveness of AES is widely debated and seems to depend on the study species, the surrounding landscape or a combination of both, it is clear that over 40 years of AES in Europe has done little to reverse biodiversity declines as a whole. Thus, it is suggested that the short-fallings of AES are likely due to their small-scale implementation and there is an increasing recognition that landscape-scale approaches are likely more effective (Macdonald et al., 2007; McKenzie et al., 2013).

1.4. Potential future solutions and gaps in knowledge

1.4.1. Regenerative farming

Regenerative agriculture (RA) is a term that has gained popularity in recent years. It is a farmer-led initiative and a variety of definitions exist (Jayasinghe et al., 2023; Sands et al., 2023), all of which encompass the broad aims of increasing soil health, biodiversity, ecosystem function, carbon sequestration and climate resilience. Some methods that have been proposed by farmers to achieve these objectives are reduced or zero-tillage, agro-forestry (combination of trees with crops or livestock), cover cropping (planting of a crop that is not harvested such as clover to prevent soil erosion on bare crop fields), crop-livestock integration and rotational grazing (where livestock are regularly moved to a different pasture). An increasing number of studies have assessed the effects of RA practices on soil biodiversity, with a particular focus on no-till and cover cropping, (Rehberger et al., 2023; Trickett and Warner, 2022), however, there is limited research on the effects on RA on above-ground biodiversity. Whilst current agricultural policies in the UK support some aspect of RA, these practices generally receive little government financial support in the UK (Shennan-Farpón et al., 2025) and more research is needed to evidence

future agricultural policies (The British Ecological Society, 2025). There is also a need for greater support from government policies for RA globally (Al-Kaisi and Lal, 2020).

1.4.2. Mixed farming

‘Mixed farming’, where livestock are integrated into the crop rotation is a principal of regenerative agriculture and is similar to pre-industrial revolution farming systems. Livestock can be integrated either by rotating temporary grassland around the farm, or by sowing herbal leys in arable fields that are then grazed by livestock. In addition, manure collected over the winter months when cattle are housed in barns (at higher latitudes) can be spread over crop fields for additional fertilisation. Indeed, mixed farming has the potential to reduce the need for external inputs, with studies showing that including temporary grassland into the rotation increases soil organic matter and nitrogen content (Nevens and Reheul, 2002). Furthermore, grazing livestock can help to reduce competitive weed species in arable fields when these are included in a pasture–crop rotation (Zani et al., 2021) thus reducing the need for herbicides. Pasture, when grazed at lower stocking rates (0.91 ewes per Ha, equivalent to 0.14 livestock units (LU) per Ha) can provide important habitat for insects (Evans et al., 2007). Increasing or intermediate amounts of grassland in the surrounding landscape can increase bird species richness (Smith et al., 2020) and bat activity (Monck-Whipp et al., 2017). In addition, pasture can provide a more permanent habitat for overwintering arthropods (Schmidt and Tschardt, 2005) than arable fields that are often ploughed in the autumn. In fact, ploughing, tilling and other mechanical practices associated with crop management can reduce invertebrate abundance by up to 60 % compared with unploughed fields (Thorbek and Bilde, 2004). However, grazing livestock can also have negative impacts on invertebrates, particularly at higher stocking rates (0.4 LUs per Ha; Littlewood, 2008). Thus, the effects of mixed farming on

biodiversity could be both positive and negative and are likely complex, operating at a range of different scales (Figure. 1.4). In UK agricultural policy there is currently no financial incentive to adopt mixed farming, though farmers often adopt this farming system to reduce costs of inputs and diversify income (Meunier et al., 2024). Mixed farming may also allow farmers to maximise income by grazing livestock on parts of the farm that are less suitable for crops (e.g. areas with shallow soils or that are prone to flooding).

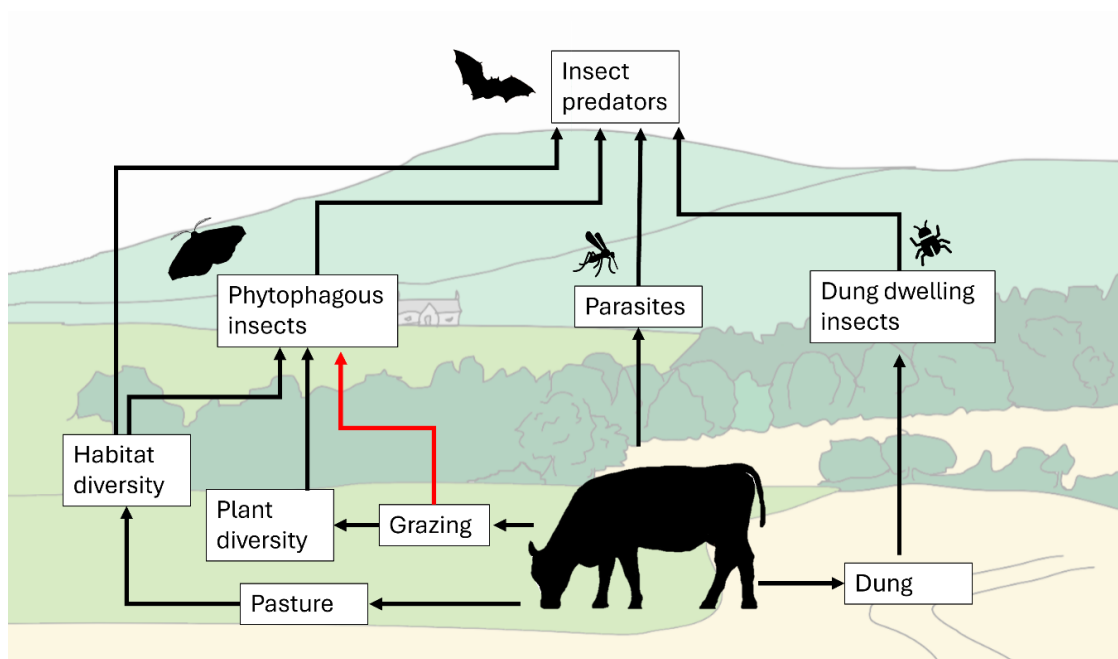


Figure 1.4. Path diagram showing potential direct and indirect benefits of integrating livestock on insects and higher trophic levels such as bats.

1.5. Moths

1.5.1. Moth ecology

Moths (Lepidoptera) are one of the most biodiverse insect orders, with around 2,800 different species occurring in the UK alone (Agassiz et al., 2024) and over 160, 000 worldwide. Moths adopt a variety of survival strategies with some species overwintering as eggs, others as larvae and some overwintering as adults, meaning that moths with different survival strategies may respond differently to environmental stressors (Littlewood, 2008; Uhl et al., 2021) .

Lepidoptera in their larval stage are usually phytophagous or detritivores, whilst adults usually feed on nectar or may not feed at all (Waring and Townsend, 2018). Adults can be highly mobile with some species able to migrate thousands of kilometres (Mz et al., 2021; Reppert and de Roode, 2018). The habitat requirements of moths in their larval and adult stages can be very different, with larvae of some species requiring a very specific foodplant. This makes moths a functionally diverse insect group.

Whilst the economic value of this pollination service has been less studied than for diurnal insects (Macgregor and Scott-Brown, 2020), it is clear that moths provide a significant pollination service to wild flowers (Anderson et al., 2023; Walton et al., 2020) and have the potential to provide economically important pollination services to crops and plants of conservation concern (Buxton et al., 2022). Moths are also an important food source for bats and birds. In fact, caterpillar abundance has been positively associated with fledgling weight and chick numbers for great tits (Pelech and Hannon, 1995). Furthermore, herbivorous larvae can facilitate nutrient cycling (Kaukonen et al., 2013) and many micro moth species are also decomposers, further contributing to nutrient cycling (Nasu et al., 2012).

1.5.2. Conservation status of Lepidoptera

Several countries worldwide have monitoring programmes for Lepidoptera that have led to a good understanding of population fluctuations in various parts of the world. For example, drawing from data across 35 monitoring programmes in the USA, (Edwards et al., 2025) conclude that overall abundance of butterflies declined by 22% since the year 2000. In addition, 13 times as many species were declining than were increasing in abundance. Population declines of butterflies and moths have also been seen using long-

term datasets across various parts of Europe (Burner et al., 2021; Valtonen et al., 2017)

In the UK, moths are one of the most well-studied insect orders, with a long-term monitoring system in place since 1964 (Bell et al., 2020). Because of this long-term monitoring clear population and distribution trends have been established for many species. Based on this long-term data, UK moth abundance over the last 50 years has significantly declined by 33%, with four times as many moth species having decreased than have increased (Fox et al., 2021). Whilst moth abundance is in decline, distribution ranges for some species seem to be expanding. Indeed, the number of species of moths in the UK has increased since 1900, largely due to the arrival of an additional 137 species that have expanded their range from southern Europe (Fox et al., 2021). However, many species are declining in both abundance and distribution, with moorland species seemingly worse affected than moths from other habitat types (Fox et al., 2021). Despite over 40% of larger moth species seeing significant population declines in the UK (Fox et al., 2021), there are currently very few laws to protect them, with just eight species designated a protection status. Whilst moths and butterflies may benefit from protected areas such as nature reserves (Brereton et al., 2008; Howe et al., 2004), some studies note severe declines even within these protected areas (Baker et al., 2016; Hallmann et al., 2017b), suggesting that a landscape-scale approach may be needed to reverse declines.

1.5.3. Threats to moths

Changing distributions and arrival of new species of moths to areas previously outside of their habitat range is undoubtedly due to climate change (Antão et al., 2022), though some species may be introduced via human-aided transportation (Gilbert et al., 2004; Work et al., 2005). Whilst climate change

may favour certain species, many species such as moorland, mountain or cold-adapted species may be unable to expand their range in response to warming temperature and are likely more at threat from climate change than other species (Santorufu et al., 2021; Shirey et al., 2024).

Artificial lighting at night (ALAN) along road verges and in towns and cities and light pollution from urban areas has a direct impact on both moth larvae and adults. Street lighting affects caterpillar development and reduces overall abundance (Boyce et al., 2021). ALAN can also increase predation risk and reduce reproduction rates in adult moths and other aerial invertebrates (Owens et al., 2020). Though ALAN has impacts on local insect populations the importance of this driver for wider population declines is largely unknown (Fox, 2013).

However, land-use change driven by intensive agriculture has been identified as the leading driver of moth declines alongside climate change (Fox, 2013; Fox et al., 2014; Wagner et al., 2021). Various aspects of intensive farming have a negative impact on moth diversity or abundance. High stocking rates of cattle or sheep are associated with intensive livestock farming. Whilst grazing livestock can be beneficial for plant diversity and the phytophagous insects that rely on it (section 1.4.2), livestock grazed at high stocking rates almost always reduces diversity and abundance of Lepidoptera compared with fields grazed at lower intensities (Littlewood, 2008; Pöyry et al., 2006; Van Noordwijk et al., 2012). Thus, moths are regularly found to respond to differences in grassland and livestock management. In addition, diurnal Lepidoptera are good indicators of wider biodiversity in grassland systems (Erhardt, 1985).

Adult moths are highly mobile and frequently respond negatively to homogenisation of agricultural landscapes (Ekroos et al., 2010; Mangels et al., 2017) and a low proportion of semi-natural areas (Fuentes-Montemayor et al., 2011a). Low landscape connectivity may also drive moth declines (Ekroos et al.,

2010), with hedgerows providing important floral resources and shelter for adult moths (Merckx et al., 2010).

Finally, some species of moth can cause considerable crop damage in their larval form. For example, the diamond back moth (*Plutella xylostella*) and the African army worm (*Spodoptera exempta/exigua*) can wipe out entire crop fields (Prinsloo et al., 2015). These outbreaks are often prevented or dealt with by the use of pesticides which likely have a toxic effect on non-target Lepidoptera (Pisa et al., 2015b). Not only do synthetic fertilisers reduce the diversity of plant food and nectar sources available for moths (Liu et al., 2025), they can also reduce the number of flowers produced by plants (Dupont et al., 2018) and can have a direct toxic effect on moth caterpillars (Kurze et al., 2018).

The high diversity of moths and that fact that they have been well-studied in the UK (both in terms of their response to environmental drivers and their life histories and feeding strategies) make them a good study group for assessing the effects of agricultural systems on biodiversity.

1.6. Bats

1.6.1. Bat ecology

Chiroptera is one of the most diverse orders of mammals, with at least 1,498 species worldwide (Simmons and Ciranello, 2025). The vast majority of bat species are nocturnal and will 'roost' in hollow trees, caves and built structures, such as roofs or tunnels during daylight hours. These nocturnal species have adapted to hunting at night, with at least 700 species, of the sub-order Microchiroptera using echolocation to navigate and find food.

Bats across the globe have a range of feeding strategies, from nectar-feeders to frugivorous bats to hematophagy and even carnivorous bats. However, over 70% of bat species worldwide, and all UK species, are insectivores, feeding on a variety of nocturnal invertebrate orders. In Scotland

the most common species *Pipistrellus pipistrellus* (common Pipistrelle), *Pipistrellus pygmaeus* (soprano Pipistrelle), *Myotis daubentonii* (Daubenton's bat) and *Myotis Nattereri* (Natterer's bat) feed mainly on Diptera (Barlow, 1997; Swift et al., 1985; Vesterinen et al., 2018, 2016) whilst another common species, *Plecotus auritus* (brown long-eared bat), feeds mainly on Lepidoptera (Andriollo et al., 2019). Insectivorous bats have been found to consume up to 30 % of their body weight in one night in their natural environment (Pimentel et al., 2022), with evidence that some species are able to reduce crop damage from insect pests (Puig-Montserrat et al., 2020; Sierra-Durán et al., 2025; Tuneu-Corral et al., 2024).

Bats at higher latitudes, including all UK species, hibernate during colder months of the year when insects are scarce, occasionally emerging to feed on warmer nights (Frafjord, 2021a; Park et al., 2000). During this time bats will often hibernate in groups and many species will favour underground caves or cellars where temperatures remain more stable than above-ground roosts. The length of time that bats spend in hibernation depends on species, latitude and weather, but in the UK bats are known to enter hibernation between September and October and will begin to emerge from this state of torpor between March and April (Racey, 1973). In May to June female bats form maternity roosts and give birth to pups that were conceived in the autumn. Pups are reliant on their mother's milk until six weeks old (around August), when they are able to feed themselves and will forage for insects in close proximity to the maternity roost. In the autumn (September – October) females will mate again, often leading to increases in social calls at this time of year (Russ et al., 2003a).

Most bats will forage in sheltered areas such as woodland, woodland edges or hedgerows. Mature broadleaf woodlands are also important for bats as they can provide hollow trees for roosting. Many species of bat in the UK actively avoid urban areas and areas that are lit (Mathews et al., 2015a), although *P. pipistrellus* is known to forage around street lights (G. Rowse et al., 2018) and some species are known to make opportunistic use of buildings for

roosting (Jenkins et al., 1998). In addition, insectivorous bats have adapted a number of different foraging strategies dependant on the surrounding habitat and associated insects (Aldridge and Rautenbach, 1987; Neuweiler, 1989; Norberg et al., 1997):

Open-space foragers: these bats have adapted to forage in open spaces using fast flight and long-range echolocation. These bats forage well above the woodland canopy, making them less susceptible to habitat fragmentation and landscape barriers such as roads and agricultural fields. In my study area, open-space species are rare, though slightly further south there are frequent records for *Nyctalus nyctalus* and *Nyctalus leisleri* (with sporadic records of this species in my study area).

Clutter-adapted or narrow-space foragers: These bats tend to have lower wing loading ratio than open-space foragers to increase manoeuvrability in highly cluttered areas such as woodland (Senawi and Kingston, 2019). Their echolocation signals are usually quieter to above echo from nearby objects. Thus, these bats have discriminatory close-range sensory perception and they are often able to 'glean' arthropods from vegetation, water surfaces and even from the ground (Anderson and Racey, 1993). In Scotland *Myotis Nattereri*, *Myotis daubentonii* and *Plecotus auritus* are all clutter-adapted species.

Edge adapted: Edge-adapted bats are between open-space and clutter-adapted species. They are often found foraging along woodland edges or hedgerows. In my study area, edge-adapted species consist of *Pipistrellus pipistrellus*, *Pipistrellus pygmaeus* and *Pipistrellus nathusii*. These species all use aerial-hawking, catching flying insect prey mid-flight.

1.6.2. Conservation status of bats

Globally, almost a quarter of all bat species assessed by the IUCN have been given a threatened status, with data lacking for 18% of assessed species

(IUCN, 2025). In Europe this trend is similar, with 17 out of 49 species considered threatened. Of the 18 bat species known to breed in the UK, two species are classified as critically endangered or endangered, two are considered vulnerable and a further two species are near-threatened in Britain. In Europe, bats are thought to have suffered substantial declines over the past century (Stebbing and Griffith, 1986). However, whilst anecdotal evidence suggests that bats across Europe are still far from historic population numbers, many species populations have shown signs of recovery in recent years and populations of these species are currently considered stable in Britain (Barlow et al., 2015). Reasons for recovery of population numbers are unclear but may be attributed to the protections put in place since 1981 by the Wildlife and Countryside Act in UK (Browning et al., 2021) that have made the damage and destruction of bat roosts illegal. All bat species have also been legally protected in Europe since 1991 by the Agreement on the Conservation of Populations of European Bats (EUROBATS, 1991) and similar recovery of populations of certain species has been noted (Van der Meij et al., 2015) though not all European bat species population trends have been assessed.

1.6.2. Threats to bats

The current biggest known threat to bats globally is agriculture, with many species threatened by both small holder farming (mostly in tropical and sub-tropical regions) and intensive agriculture as well as land-use change from changes in farming practices (IUCN, 2025). Other important threats include urbanisation and industrial activities such as quarrying, with many bat species also under threat from persecution (IUCN, 2025).

Bats respond negatively to increasing amounts of agricultural land cover in the landscape (Monck-Whipp et al., 2017; Put et al., 2019), with some species found to avoid arable fields (Nicholls and Racey, 2006). In fact, bat activity in

agricultural landscapes is mostly associated with remnants of semi-natural habitat such as broadleaf woodlands (Davidson-Watts and Jones, 2006a; Fuentes-Montemayor et al., 2013; Heim et al., 2015), linear woody features such as hedgerows and treelines (Blary et al., 2021; Lentini et al., 2012), semi-natural grassland and extensively managed pastures (Ancillotto et al., 2023; Starik et al., 2019) and water (Nicholls and Racey, 2006). Thus, the removal of these habitats associated with intensive farming is likely to have contributed to population declines.

Intensive agriculture is also associated with widespread use of insecticides, which have negative effects on a wide range of non-target insects. Pesticides are known to cause deformities in Diptera (Madden et al., 1992), with a case-study showing that cessation of intensive tobacco farming (along with ceasing of pesticide applications) led to a reduction in larval deformities of non-biting midge larvae sampled in streams (Gagliardi and Pettigrove, 2013). It is unsurprising then that the abundance of Diptera can be negatively correlated with the number of pesticide applications (Olimpi * and Philpott, 2018). This reduction in insect abundance from widespread insecticide use has implications for insectivorous bats. Not only does this practice reduce the availability of food, it also increases the risk of insectivorous animals to bioaccumulation (the gradual build-up of a substance in an organism) of harmful chemicals. Harmful levels of insecticides have been found in various insectivore mammals, such as the European hedgehog (Rasmussen et al., 2024) and other small mammals (Fritsch et al., 2022), but also in birds and bats (Bouwman et al., 2008; Khan et al., 2014). A study by (Valdespino and Sosa, 2017) found evidence of bioaccumulation of agrochemicals in fruit bats, with increasing numbers of studies finding the presence of insecticides in both bat guano and body parts of insectivorous bats too (Afonso et al., 2016; Bayat et al., 2014). This risk of exposure to toxic insecticides is poorly understood and requires further research (Brooks et al., 2021).

Though there is still a lack of research to support the use of bats as indicators of biodiversity (Park, 2015; Russo et al., 2021), the consistent negative response of bats to intensive agriculture and their reliance on insect prey availability makes them a good candidate species for studying the effectiveness of farming approaches to reverse biodiversity decline.

1.7. Thesis outline and aims

Intensive farming practices and associated changes in agricultural landscapes are key drivers of widespread and precipitous declines in biodiversity. If we are to reverse these declines, meet legally binding biodiversity targets and preserve functioning ecosystems we need strategies that work for a variety of species and at a larger scale. Nocturnal insects such as moths provide important ecosystem services and are a well-studied and diverse taxonomic group, making them an ideal candidate for understanding the impact of farming practices. Bats are limited by the availability of their insect prey. Most species are highly mobile, therefore are likely to respond to landscape-scale initiatives. The purpose of this thesis is to investigate the impacts of two farming systems (that have been proposed as solutions to increasing biodiversity on farms) on nocturnal insects and bats. The broad aims of this study are:

1. To assess the benefits of mixed farming in comparison to arable farming on bats and nocturnal insects and to disentangle direct effects from indirect effects mediated by local and landscape features (Chapters 2, 3 and 4).
2. To assess the benefits of a regenerative grazing practice on moths (Chapter 5)

Chapter 2: Does mixed farming benefit moths? Exploring how different farming systems shape both local features and the wider landscape.

A version of this chapter has been published as:

Kennedy, R., Fuentes–Montemayor, E., Park, K.J., Littlewood, N., 2026. Does mixed farming benefit moths? Exploring how different farming systems shape both local features and the wider landscape. *Agric. Ecosyst. Environ.* 396, 109996. <https://doi.org/10.1016/j.agee.2025.109996>

CRedit authorship contribution statement

Rochelle Kennedy: Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Elisa Fuentes–**

Montemayor: Writing – review & editing, Validation, Supervision, Resources, Methodology, Conceptualization. Project administration. **Kirsty J**

Park: Writing – review & editing, Validation, Supervision, Resources, Project administration. **Nick Littlewood:** Writing – review & editing, Validation,

Supervision, Software, Project administration, Methodology, Funding acquisition, Data curation, Conceptualization

Abstract

Lepidoptera are important pollinators and provide an essential food source for higher taxa, yet many species that were once widespread are in decline across Europe. This is largely due to practices associated with intensive farming, such as pesticide and fertiliser applications and habitat loss. There is increasing interest in finding ways of farming that are beneficial to both humans and biodiversity. 'Mixed' farming, where livestock are integrated into the crop rotation, is thought to provide benefits to biodiversity by reducing synthetic inputs and by increasing habitat and crop diversity. However, at commercial stocking levels, livestock can have detrimental impacts on grassland Lepidoptera. I investigated the different pathways through which mixed farming could benefit moths in comparison to arable farming (where livestock are absent). Between June and August 2022, twenty-six farms in Scotland were surveyed for moths using light-trapping. Mixed farming indirectly benefitted micro moths by increasing woodland edge density. Positive effects of woodland were also observed for 'farmland' micro moths that do not feed on woody plants. However, for micro moth species richness, this positive effect of woodland edge was outweighed by a direct negative effect of mixed farming. This highlights the need for more research to find livestock management practices that are beneficial for Lepidoptera.

2.1. Introduction

The decline of insect populations in Europe since the industrial revolution has been well documented, with evidence that similar declines are taking place elsewhere across the globe (Outhwaite et al., 2022; Wagner, 2019). The United Kingdom (UK) is no exception to this trend, with declines reported for native bees (Biesmeijer et al., 2006; Powney et al., 2019), ground beetles (Brooks et al., 2012), butterflies (Warren et al., 2001) and moths (Fox et al., 2014).

With over 2,500 different species in the UK, moths are a highly diverse group of insects and declines in their diversity and abundance may be indicators of a wider biodiversity crisis (Gerlach et al., 2013). Moth population declines and species loss also have serious implications for pollination services (Walton et al., 2020) and will likely impact on a variety of taxa at higher trophic levels for which they are an important food source (Aldasoro et al., 2019; Vickery et al., 2001). Additionally, moth population declines in the UK are not only affecting specialist and rare species but also some of the most common and widespread moths (Fox et al., 2021).

Intensive agricultural practices are thought to be one of the key drivers of moth declines in the UK (Fox, 2013). They are characterised by landscape simplification (e.g. through widespread crop monocultures and the removal of hedgerows and semi-natural areas) and the extensive use of synthetic fertilisers, herbicides and pesticides (Mazoyer and Roudart, 2006). These less diverse landscapes have been associated with lower moth diversity (Botham et al., 2015). The reduction in crop diversity itself may also have negative impacts on insects due to reduced diversity of food resources both spatially across the surrounding landscape and temporally throughout the season. There is evidence in some parts of Europe that areas with higher crop diversity are associated with higher moth species richness (Novotný et al., 2015). However, in the UK, the requirement for farmers to grow at least three different crop types

on their land in order to receive government subsidies was removed in 2021, potentially leading to a further increase in crop monocultures.

The widespread use of synthetic inputs on farms is a major driver of declines for insects, including moths. Application of insecticides can be fatal for Lepidoptera (Pisa et al., 2015), whilst high nitrogen input and the use of herbicides may have an indirect negative impact on moths by reducing the abundance and diversity of plant food available in field margins (Dupont et al., 2018). Alarming, recent research has shown that the UK's current levels of nitrogen input on agricultural land directly reduces the survival rate of six common moth species by at least one third (Kurze et al., 2018). This is potentially due to the increased amounts of nitrogen in the hostplant being above the physiological tolerance of these Lepidoptera species.

Organic farming, where synthetic inputs are excluded entirely, could reduce the impacts of farming on insects. However, studies have found mixed results on the effects of organic farming on moths with both positive outcomes (Wickramasinghe et al., 2004) and no effect (Boutin et al., 2011; Jonason et al., 2013). In addition, organic farming currently only covers 3% of the total farmed area in the UK (UK government, 2023). This low uptake suggests that organic farming is unlikely to become a landscape-scale solution to biodiversity declines unless substantial changes in policy take place to support farmers.

Agri-environment schemes are another proposed solution where farmers are given financial incentives to manage certain areas of a farm in an environmentally friendly way (e.g. maintaining patches of semi-natural areas or leaving field margins untreated), but are able to manage the rest of the farm intensively. This approach has been implemented in Europe for over forty years. Though some of these incentives are beneficial for moths (Fuentes-Montemayor et al., 2011) they have done little to reverse widespread population declines, potentially due to not being implemented at large enough scales to benefit this highly mobile taxonomic group.

There are, however, other system-scale approaches with the potential to mitigate the negative effects of intensive agriculture. Mixed farming is the practice of integrating livestock into the crop rotation by rotating arable crops with temporary grassland that is grazed by livestock. This has the potential to increase habitat diversity at the landscape scale by balancing areas of arable crops with areas of grassland and may also prompt farmers to grow a wider range of crops to feed livestock. Mixed farms may also be more likely to retain areas of woodland that can act as shelter for livestock during the winter months. Woodland fragments in agricultural landscapes are beneficial both for woodland specialists (Fuentes-Montemayor et al., 2022, 2011) and grassland moth species (Kühne et al., 2022). Livestock also provide natural weed control to agricultural fields, reducing the need for synthetic herbicides (MacLaren et al., 2019). The natural nutrient input from livestock dung and the rotation of temporary grasslands with arable crops can reduce the amounts of synthetic fertiliser required for growing crops (Nevens and Reheul, 2002). In addition, grazing is an important part of the grassland ecosystems, helping to control competitive plant species, thus maintaining plant diversity (Kapás et al., 2020; Krüss and Tschardt, 2002). Though grazing livestock can increase the diversity of plant food available for phytophagous insects, the impacts of grazing on Lepidoptera in particular are often found to be negative, especially when pasture is grazed at higher stocking rates (Littlewood, 2008; Pöyry et al., 2004). This negative effect could be attributed to competition for food between grazing livestock and plant-feeding Lepidoptera, and/or trampling and accidental consumption of Lepidoptera by livestock. In addition, the vast majority of research on the impacts of grazing on moths has been conducted on permanent pasture (> 5 years old). However, pasture on mixed farms, due to its rotation with crops, is likely to be largely temporary (< 5 years old) and potential benefits to moths may be reduced or negated due to regular disturbance, though this has been understudied. Thus, mixed farming could have both positive and negative effects on moth abundance and diversity.

These effects could also be either direct or indirect mediated by landscape-scale attributes (e.g. habitat diversity) or local features influenced by management (e.g. hedgerow height; Figure 1). However, the overall effects of mixed farming systems on moths remain poorly understood and there is limited evidence to ascertain whether this farming system should be recommended as a route to increasing insect diversity on farms.

This study takes a whole-system approach to investigate whether mixed farming is beneficial for moth abundance and diversity in the UK when compared with 'arable' farming, where livestock are absent. I addressed four questions:

Q1: Do local and landscape-scale features of mixed farms differ from those of arable farms, and, if so, do these indirect pathways have positive or negative effects on moth abundance and diversity?

Q2: Are there any positive or negative direct effects of mixed farming in comparison to arable farming on moth abundance and diversity and when combined with indirect effects is the overall effect of mixed farming positive or negative?

Q3: At the mixed farm level, does moth abundance, richness and diversity differ between cropped and mixed areas?

Q4: How is moth community composition affected by farm type, landscape-scale and local-scale features?

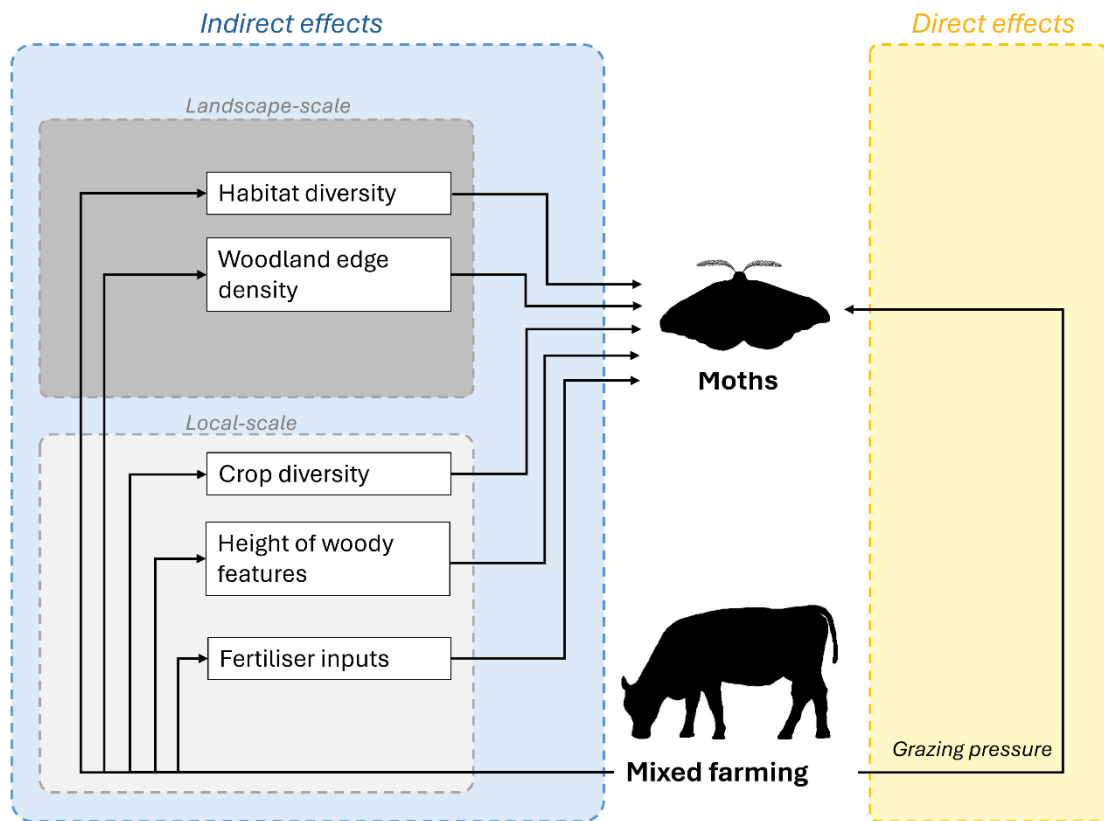


Figure 2.1: Conceptual model showing potential pathways through which mixed farming could influence both local (light grey box) and landscape (dark grey box) features with indirect impacts (blue box) on moths, as well as a potential direct pathway (yellow box) between mixed farming and moths.

2.2. Method

2.2.1. Site selection

Thirteen arable and 13 mixed farms were selected across North-East Scotland. This area was chosen as it is one of the most productive areas in Scotland for a variety of crops but also has a combination of both arable and mixed farms. Each mixed farm was paired with a nearby arable farm (min distance 3 km, max distance 16 km) to reduce the effects of weather differences between pairs. 'Arable' farms grew at least one cereal crop and had no livestock whilst mixed farms grew at least one cereal crop, with grazing livestock integrated into the crop rotation. In addition to this, all farms were required to be

growing a minimum of two different crop types to enable analysis of crop diversity. All mixed farms were rearing cattle for beef, with six out of thirteen mixed farms also grazing sheep on pasture over the winter months. Livestock were integrated by rotating temporary grassland around the farm but also included areas of permanent grassland (> 5 years old). Additionally, some farms also sowed brassicas or herbal mixes into arable fields that were then grazed. Stocking density on mixed farms ranged between 1.2 and 4.9 cattle per hectare, with a mean of 2.7 cattle per hectare. Farmers were recruited by using agricultural contacts at Scotland's Rural College, social media advertising and contacting farms with publicly available contact details. Further farmers were recruited by asking those already participating for recommendations.

2.2.2 Moth trapping

Moths were light-trapped on one night on each farm between mid-June and mid-August 2022. This is the peak time of year for moth abundance and species richness in Scotland and also avoids disruption from harvest taking place from mid-August onwards. Each farm within a pair was surveyed on the same night. Ultra-violet LED bucket traps were used to trap moths based on the design used in Infusino et al., (2017); these were activated by a solar sensor and run from dusk until dawn. Trapping was only carried out when temperature at sunset was above 10°C and wind speed was under 20km hr⁻¹ (estimated using the Beaufort scale). Moths use sheltered field edges such as hedgerows to navigate agricultural landscapes (Coulthard et al., 2016). Therefore, traps were placed on the edges of crop fields next to hedgerows, treelines or woodland strips (hereafter named 'woody features') to maximise catches. Though placing traps next to these features may increase the likelihood of catching moths that have travelled from the wider landscape, this was accounted for by including landscape-scale habitat features in statistical analysis (section 2.3). On each farm (both arable and mixed), three moth traps

were placed in field margins bordered by arable crops on either side (or 'crop-crop' margins; Figure 2.2). An additional three traps were placed on the edges of crop fields next to pasture ('grass-crop' margins) on mixed farms only, giving a total of three traps on each arable farm and six traps on each mixed farm. Where traps were placed in 'grass-crop' margins, presence or absence of cattle in the pasture field was recorded. Moth traps were always on the edge of a cereal field (spring barley or winter wheat, as these were consistently present across all farms) to reduce the effects of different crop types and were also located roughly halfway along the field edge, with a minimum of 100m distance between traps to reduce interference (Truxa and Fiedler, 2012).

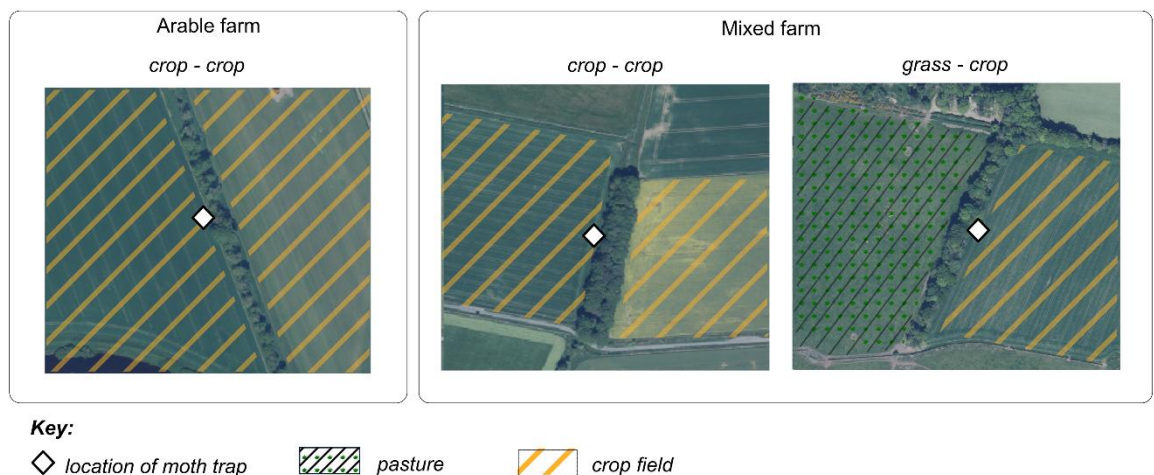


Figure 2.2: Example locations of moth traps placed on both studied farm systems in between two crop fields (crop – crop margins) and between pasture and crop fields (grass – crop). Maps were created using Vertical Aerial Imagery (2020).

Moth traps were collected within 1.5 hours after dawn and insects were euthanised by placing a cotton wool pad soaked in ethyl acetate inside each trap. Traps were then sealed for twelve hours and transported back to the lab for insects to be identified at a later date. I differentiated between macro (larger moths) and micro (smaller moths) according to classification by Waring and Townsend (2018) and Sterling and Parsons (2018). Macro moths were identified to species using Waring and Townsend (2018). Micro moths were

identified to species level where possible using Sterling and Parsons (2018), otherwise these were identified to genus or family. Micro moths that could not be identified by the first author were given to an expert for identification (see acknowledgements). Furthermore, moths were classified into guilds based on their larval foodplant type with reference to guidebooks (Sterling and Parsons, 2018, Sterling and Henwood, 2020). Macro and micro moths were classed as 'farmland moths' if their larval foodplant is found in agricultural fields (either pasture or arable) such as grasses, arable or pasture weeds, crops, or mosses (moss was included since it is often present in grasslands and could be affected by herbicides, fertiliser and grazing). Moths whose larvae feed on woody plants such as shrubs and hedgerow species were categorised as 'woody feeders'. A small number of moth species feed on both grasses and woody plants and were classed as having a 'broad diet', whilst moths whose larvae only feed on one species of plant were classed as 'specialists'. Any moths that did not fit these guilds were classed as 'other' (aquatic species for example). However, only 'farmland' moths contained enough data for analysis by guild. Hill diversity (hereafter referred to as 'diversity') was calculated for macro moths, micro moths, farmland macro moths and farmland micro moths using the *hillR* package in R (Li, 2018).

2.2.3. Landscape analysis

QGIS version 3.28.1 (QGIS, 2021) was used to create buffers of 250 m, 500 m and 1000 m radius around the location of each light trap as these spatial scales have been found to be most relevant to both macro and micro moths (Fuentes-Montemayor et al., 2011; Merckx et al., 2012). The UK Centre for Ecology and Hydrology Landcover Map (Marston, 2021) was used to quantify the proportion within each buffer covered by buildings, improved grassland, arable, woodland, semi-natural (combined semi-natural grassland, rough-

grazing, scrub, moorland and wetland), coastal habitat and water. In addition, the distance of each trap from the nearest freshwater body was measured using OS MasterMap (2023). Crop maps supplied by farmers were used along with ground-truthing to obtain the proportion of total land covered by each crop type. This was done within a 250 m radius of each trap, as this was the largest scale possible without including fields that were outside of farm boundaries. Crops were grouped into the following categories, as some crops may provide similar resources: cereals, legumes, root vegetables, brassicas, grass, agri-environment scheme seed mix and 'other' (Table S.2.1.). The landscapemetrics package (Hesselbarth, 2019) in R version 4.3.2 (R Core Team, 2023) was used to calculate woodland edge density (broadleaf and coniferous combined), the proportion of each land cover type within each buffer, Shannon's index for habitat diversity and crop diversity. An R-squared value for each landscape metric at each different scale was calculated by building linear models (for diversity data) or general linear models (for count data) using the R packages lme4 and MASS (Bates et al., 2015; Venables and Ripley, 2002). Models were built separately for abundance, richness and diversity of all macro moths, all micro moths, farmland macro moths, and farmland micro moths. Nagelkerke's pseudo R-squared (Nagelkerke, 1991) was used for count data with a negative binomial distribution since all count data was overdispersed. Woodland edge density within 250 m from traps was very low on most farms (the mean proportion of woodland within 250 m of traps was 3.8%, with almost half of traps having less than 1% woodland cover within 250 m), therefore only scales of 500 m and 1000 m were considered for this metric. Similarly, the proportion of built-up areas in the landscape was negligible (even at the 1000 m scale mean urban cover was just 3.5%, with 82/111 traps having less than 1% urban cover), whilst the proportion of semi-natural areas was also low at all scales (mean >0.02% at the 1000m scale), so neither was considered for inclusion in landscape analysis. Since traps were placed between agricultural fields, the number of different land cover types at

small scales was also low. As such only scales of 500 m and 1000 m were considered for habitat diversity. As multiple landscape variables correlated with each other (Table S.2.2) and for simplicity of models, two landscape metrics were chosen for inclusion in subsequent models. Woodland edge density at 1000 m correlated negatively with the proportion of arable at the same scale (Pearson = - 0.59) but produced a higher R squared value for most moth models (Table S.2.3.), so was retained as a measure of landscape configuration, whilst habitat diversity at the 1000 m scale was retained as a measure of landscape composition.

2.2.4. Local features

Woody features that separate field boundaries such as hedgerows or lines of trees may provide different resources and varying levels of shelter for moths (Froidevaux et al., 2019). As such, the woody feature adjacent to each moth trap was categorised as 'hedgerow' (continuous row of woody plants with no mature tree species), 'treeline' (continuous line of non-coppiced tree species), or 'woodland strip' (patch/line of trees between two fields that was greater than 15m wide (min 26 m, max 128 m), as measured in QGIS using Vertical Aerial Imagery (2020)). In addition to this the maximum height of the woody feature within 15 m either side of the trap was visually estimated in the field (always by the same surveyor) and the occurrence of each woody plant species within 15 m either side of the trap was recorded.

As a measure of whether mixed farming was associated with reduced synthetic fertiliser inputs on my study site, I also asked farmers to provide information on inputs for spring barley and winter wheat for the year of 2022, as these two crops were consistently present across almost all farms. However, only 11 out of 26 farms provided sufficiently detailed information on fertiliser input. Thus, it was not possible to incorporate these data in statistical analysis, but information is provided as a supplement in Table S.2.4.

2.2.5. Statistical analysis

All statistical analysis was carried out in R version 4.3.2.

2.2.5.1. Metamodel specification

Farming strategies can influence both local features (such as the quality of hedgerows) and landscape-scale features (for example, the proportion of habitat types available in the wider landscape). In addition, farming strategies could have both positive and negative impacts on moths, either directly or mediated by different pathways. To help understand the various pathways through which mixed farming could benefit moths and the overall effect of mixed farming (Q1 and Q2), a causal network approach was taken. Structural equation modelling (SEM) was used to compare moth abundance, species richness and diversity between mixed and arable farms using the *piecewiseSEM* package (Lefcheck, 2016). SEMs are a multivariate technique that test the significance of direct and indirect pathways in a causal network system. SEM also allows a comparison of the relative effect size of different predictor variables (Grace et al., 2010). For a fair comparison between arable and mixed farming systems overall, only traps placed along crop-crop margins were used for SEM analysis ($n = 72$). Traps placed next to pasture ('grass-crop') were included in subsequent mixed effects models for mixed farms only (section 2.5.2) to address Q3. I constructed an initial SEM metamodel which included landscape and local-scale features that have previously been identified in the literature as relevant to moths as well as my variables of interest (farm type and crop diversity; Figure.2.3). High landcover diversity is known to benefit moths (Ekroos et al., 2010) and was included in my SEMs at a scale of 1000 m, as this was found to be most relevant to moths in my study (section 2.3.) Woodland in agricultural landscapes can be of benefit to both woody plant-feeding moths and grass-feeding moths (Froidevaux et al., 2019;

Kühne et al., 2022). Hence, woodland edge density within 1000 m was also included in all models. In addition, local woody features next to traps may provide shelter for moths navigating very open agricultural landscapes. I measured 'woody feature' both in terms of feature height and feature type. However, woody features classified as 'hedgerows' were significantly lower in height than those classified as 'treelines' or 'woodland patches' (Anova $p < 0.0001$), so I included the continuous variable of woody feature height in SEMs. Temperature was also included as a predictor variable to account for changes in moth emergence numbers throughout the season (Jonason et al., 2013). As there were multiple moth traps per farm, I included 'farm' as a random effect. Thus, the following fixed-effect variables were included in all SEM models: woodland edge density, habitat diversity, crop diversity, distance from water, farm type, woody feature height and temperature (Fig.3)). I built separate SEMs for all macro moths, all micro moths, farmland macro moths and farmland micro moths. For each of these categories a separate SEM was run for abundance, diversity and species richness. All continuous predictor variables were scaled by one standard deviation and centred around the mean, with the categorical variable of farm type being allocated a value of 1 for mixed farms and -1 for arable farms to enable easy interpretation of standardised model estimates. Data was log-transformed and modelled using a gaussian distribution to obtain standard coefficients for pathways as advised in Lefcheck (2021). Standard coefficients were calculated for each pathway. Where there were both direct and indirect significant pathways between mixed farming and moths, the overall effect of mixed farming was calculated by multiplying standard coefficients of each indirect pathway, then adding the standard coefficient of the direct effect (Lefcheck, 2021). A degrees of directed separation test was used to check for the presence of missing significant pathways. Where missing pathways were detected, these were included as correlated errors (Table

S.2.5.). Validity of models was confirmed by ensuring that the Fisher's C statistic was not significant ($P > 0.05$).

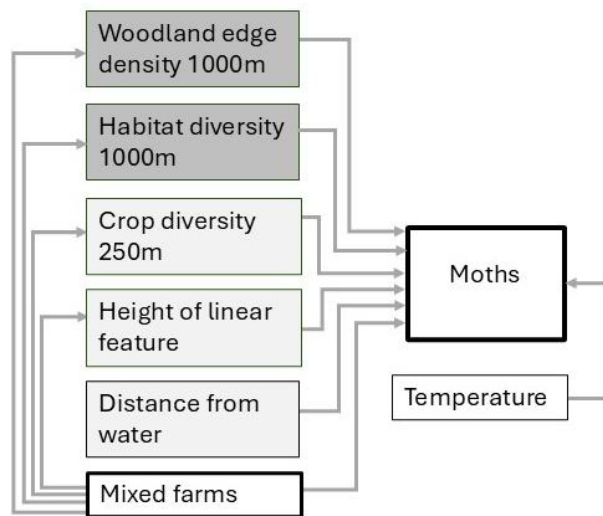


Figure 2.3: Metamodel showing all variables and pathways that were included in our SEMs. Dark grey boxes indicate landscape-scale variables whilst light grey boxes indicate local-scale attributes.

2.2.5.2. Mixed farm analysis: comparison of crop-crop and grass-crop margins.

On mixed farms, foodplant resources and synthetic inputs may differ between areas where crops are grown and areas where there is a combination of crops and grassland. To address Q3, further analysis was carried out using data collected on mixed farms only, to compare moth abundance, species richness and diversity in crop-crop traps with grass-crop traps. Mixed effects models were built in R using the lme4 and MASS packages, with moth abundance, species richness or diversity as a response variable, 'margin type' (either 'crop-crop' or 'grass-crop') as a fixed effect and 'farm' as a random effect to account for multiple samples per site. Moths were again subset to micro moths, macro moths, farmland micro moths, and farmland macro moths for these models. Landscape variables were excluded from this analysis as they were tested in SEM analysis with a greater number of sites and differences in

landscape buffers within the same farms were minimal. Similarly, 'woody feature height' was also excluded as the effects of this variable were already tested for in SEMs. All traps placed in the 'crop-crop' category had less than 20% pasture within a 100 m radius, with a mean of less than 1% pasture. Traps placed in grass-crop margins had a mean of 42% pasture within 100 m (minimum 12%, maximum 54%). I therefore used 'margin type' as a categorical predictor instead of percentage cover of crop or pasture. Thirty-five traps were placed between crop fields whilst 29 traps were placed next to pasture (a lower number of traps were placed in grass-crop margins due to less availability of this habitat on some farms).

2.2.5.3. Community analysis

Non-metric Multi-Dimensional Scaling (NMDS) was used to visualise how moth communities differ according to landscape-scale and local-scale variables (Q4). To analyse differences in moth community composition between arable and mixed farms I summed moth catches from crop-crop margins for each farm to obtain a farm-level moth community. Although I aimed to have three crop-crop traps per farm some traps malfunctioned, thus two crop-crop traps from each farm were randomly selected for this analysis (if only two traps were functional, both were automatically kept for analysis). Farm-level analysis was also used to test for the effects of landscape configuration on moth communities, as there was little variation in landscape metrics at the 1000 m scale between traps on the same farm. Of all landscape metrics considered in section 2.3., woodland edge density at the 1000 m scale was found to be the most relevant to moth abundance, species richness and diversity. As such, a mean woodland edge density at the 1000 m scale for each farm was calculated and included in farm-level community analysis. To understand how local-scale features such as pasture presence and woody feature height affect moth communities NMDS was also carried out at the

trap-level using traps from mixed farms only. Given that crop diversity was measured on a relatively small scale (250 m), this was also included as a local-scale predictor of trap-level moth community composition.

Bray-Curtis distance was used as a metric of community dissimilarity for all NMDS as this considers species abundance as well as occurrence. Singleton species (species only found in one trap) were kept as they caused no issues with NMDS convergence. NMDS plots were produced for all macro moths, all micro moths, farmland macro moths, and farmland micro moths using the vegan package in R (Oksanen, 2024). There was insufficient data on 'woody feeders' or any other guilds to achieve convergence for these groups. Data was not transformed since untransformed data gave a better stress value in all models. Two dimensions were enough to achieve a stress level of less than 0.2 which is considered the maximum stress level for an interpretable NMDS (Clarke, 1993), except for farmland micro moths at the farm level where three dimensions were necessary to achieve an appropriate stress value. Permutational multivariate analysis of variance (PERMANOVA) was conducted to test the effect of environmental variables on moth community composition using the 'adonis2' function in the vegan package with permutations set to 999. Final variables included in PERMANOVA for farm-level analysis were 'farm type' and woodland edge density at the 1000 m scale. Final variables included in trap-level analysis for mixed farms were woody feature height, margin type (crop-crop or grass-crop) and crop diversity 250 m.

2.3. Results

Across all traps (n = 110) a total of 6,801 individual macro-moths and 2,680 individual micro moths were caught. Overall, 98.8% of macro moths and 90.6% of micro moths were identified to species level, giving a total of 123 different macro-moth species and 98 different micro moth species (see Table S.6. for a full list of species). Of these, 38 macro moth species and 37 micro moth species were singletons (only found in one trap). Forty macro moth species caught were classed as having suffered significant long-term declines in abundance in the UK with seven of these now categorised as ‘vulnerable’ or ‘threatened’ on the GB red list (Cook et al., 2022). A large percentage of macro moths (77 %) and micro moths (71 %) were classified as farmland moths that feed on grasses or arable weeds in their larval form (Figure.2.4a.). Similarly, 59% of all macro moth species and 56% of all micro moth species were farmland species (Figure.2.4b.).

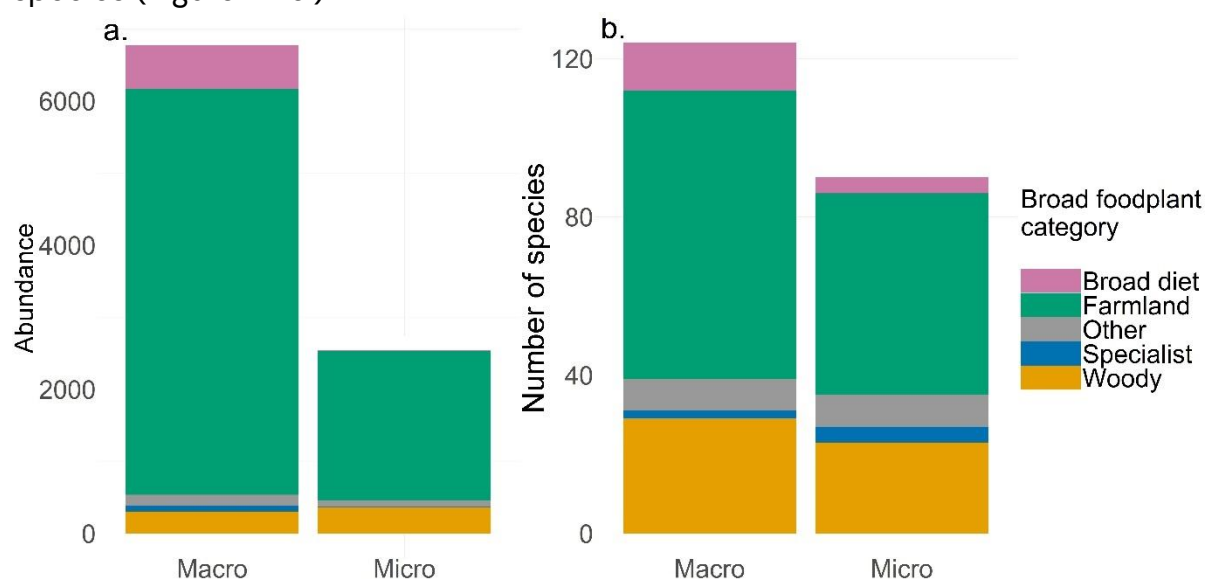


Figure 2.4: Abundance of macro and micro moths by functional group (a) and total number of macro and micro moth species included in each guild (b).

2.3.1. Direct and indirect effect of farm type on moths

2.3.1.1. Landscape composition

Farming type had a marginally non-significant effect ($0.1 > P > 0.05$) on woodland edge density within a 1000m radius of moth traps ($P = 0.06$), with mixed farms having higher densities than arable farms. Higher densities of woodland edge, in turn, significantly increased micro moth abundance and species richness and farmland micro moth abundance (Figure 2.5). An increase of just over 22m (1 standard deviation) of woodland edge per hectare increased mean micro moth abundance by 27% ($SE \pm 12\%$) and mean species richness by 19% ($\pm 7\%$). This also held true for farmland micro moth abundance with an increase of 28% ($\pm 12\%$), but not for farmland micro moth species richness or diversity, where the relationship was non-significant (Figure 2.5 & Figure S.2.1.). Macro moths were unaffected by changes in woodland edge density. Habitat diversity at the 1000m scale was unaffected by farm type. However, habitat diversity had a significant negative effect on micro moth abundance as well as a marginally significant negative effect on farmland micro moth abundance ($p = 0.07$).

2.3.1.2. Farm type

Though mixed farming indirectly positively affected micro moths by increasing woodland edge density, there was also a direct negative effect of mixed farming in some cases. Micro moth species richness was lower on mixed farms than on arable farms, with the direct effect of mixed farming reducing mean number of micro moth species by 14% ($\pm 7\%$). The combined direct and indirect effects of mixed farming in this model led to an overall negative effect for micro moth species richness (Figure 2.5). Farm type did not influence any other local or landscape-scale variables included in these models.

2.3.1.3. Local-scale features

The height of the woody feature next to traps was not driven by farm type but did have a significant positive effect on farmland micro moth abundance and a marginally significant positive effect on farmland micro moth species richness ($P = 0.09$) and diversity ($P = 0.09$). An increase of 8m in height increased mean farmland micro moth abundance by 18% ($\pm 8\%$). Crop diversity had no effect on moths.

Other influential variables that were unrelated to farming were temperature and distance from water. Temperature had a significant positive effect in almost all models and was the most influential variable in all models where it was significant, except for micro moth species richness, where woodland edge density was equally influential (Figure 5). Distance from water only affected macro moths, with abundance, species richness and diversity

decreasing with increasing distance from freshwater (Figure S2.1.). The random effect of 'Farm' also explained some of the variation in moths in all models.

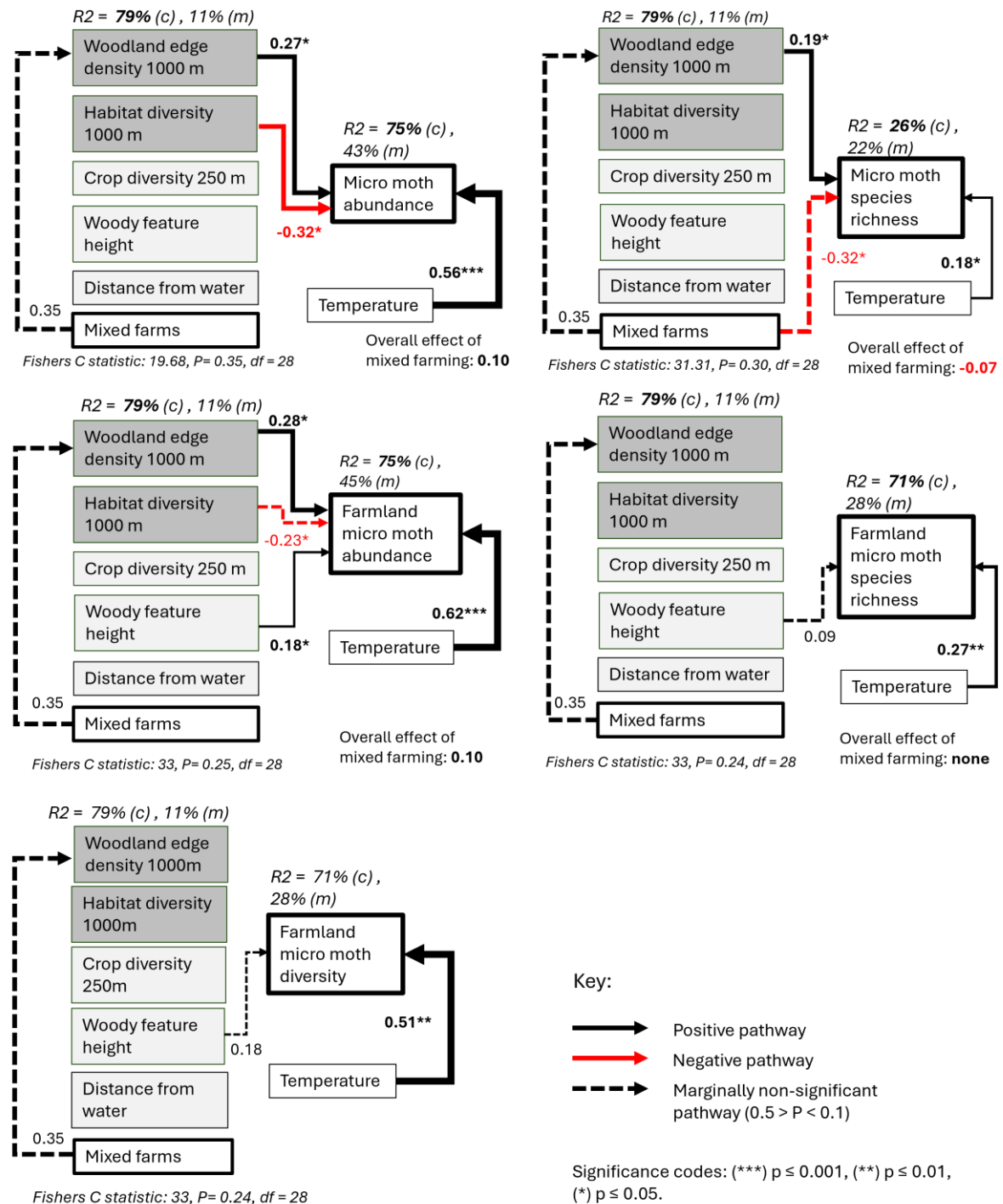


Figure 2.5: Path diagrams for all SEMs where variables of interest had a significant effect on moths. Non-significant models are provided in Figure S1 and model summaries for all SEMs are provided in table S.5. Boxes represent variables included in each model. Standard estimates for each significant pathway are given next to the corresponding arrow along with significance stars. Dark grey boxes indicate a landscape-scale variable whilst light grey boxes are local-scale variables. Significance codes: (***) $p \leq 0.001$, (**) $p \leq 0.01$, (*) $p \leq 0.05$.

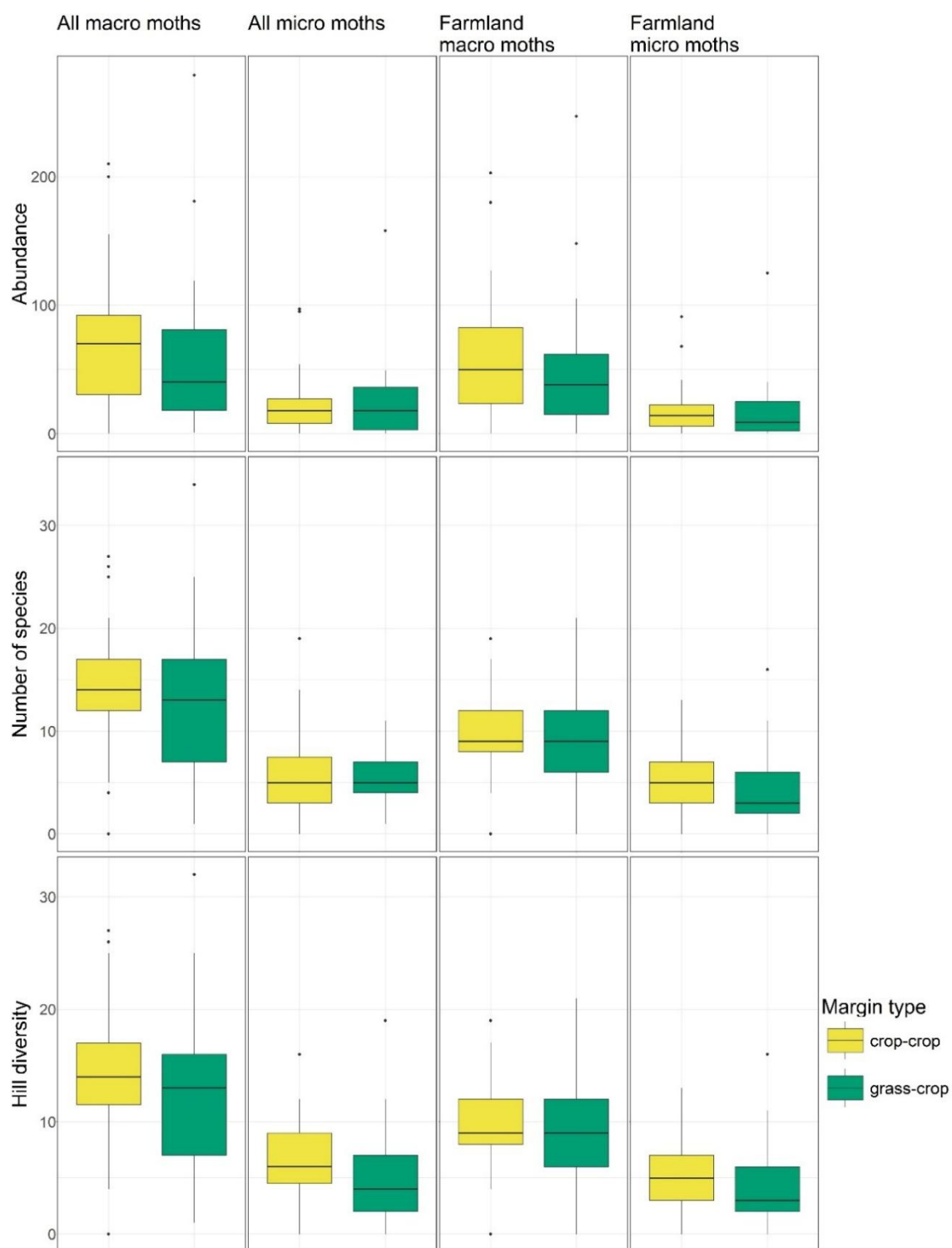


Figure 2.6: Boxplots showing differences in moth abundance, species richness and diversity between crop-crop and grass-crop margins on mixed farms. Significance codes: (***) $p \leq 0.001$, (**) $p \leq 0.01$, (*) $p \leq 0.05$, ns > 0.1 .

2.3.2. Mixed farming: influence of pasture on moths

Whilst macro moth abundance, micro moth diversity and farmland micro moth diversity tended to be lower in crop-grass margins compared with crop-crop margins on mixed farms (Figure 2.6.), margin type had no significant effect on the abundance, richness or diversity of any of the moth groups.

2.3.3. Moth community composition

2.3.3.1. Influence of landscape-scale features on community composition

NMDS plots showed no visible clustering of moth communities by farm type (Figure 2.7a, 2.7b). PERMANOVA tests revealed that there was indeed no significant effect of farm type on either macro moth or micro moth community composition. At the farm scale, micro moth community composition differed significantly across a gradient of woodland edge density within 1000 m of traps ($P = 0.04$), with woodland edge density explaining a small proportion of the variation in moth community composition (Figure 7.b). Micro moth communities associated with greater woodland edge density are situated towards the bottom of the plot whilst those associated with lower woodland edge density are located towards the top of the plot. The effect of woodland edge on micro moth communities also held true for farmland micro moths (Table S.2.8, $P = 0.04$), with no visible clustering of woody plant-feeding species in areas of greater woodland edge density (Figure S.2.2). There was no significant effect of woodland edge density on macro moth community composition (Figure 2.7a).

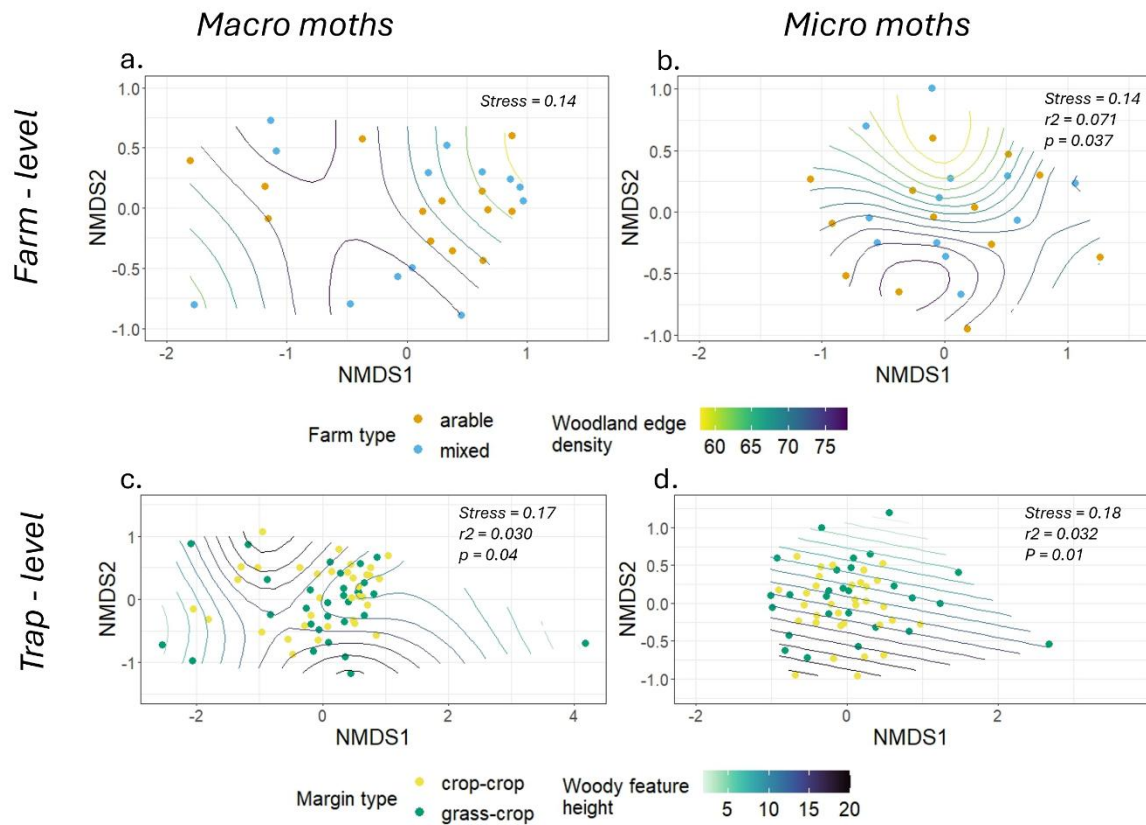


Figure 2.7. NMDS plots of moth community composition at the farm scale and at the local scale for macro moths and for micro moths. Each point represents a moth community, with points that are closer together in the plot showing moth communities that are more similar in composition than those that are further apart. Contour lines show gradients of woodland edge density (a, b) and woody feature height (c, d). P-values and r^2 values are given for the effect of woodland edge density and woody feature height on moth communities where these are significant. Values for other variables included are available in Table S.8.

2.3.3.2. Influence of local-scale features on community composition

At the local scale (trap-level), moth community composition was unaffected by field margin type (Figure 2.7c, 2.7d), with no visible clustering of moth communities found in crop-crop field margins and crop-grass margins. However, both macro moth and micro moth communities changed significantly across a gradient of woody feature height, though this only explained a small amount of the variation in the data (Figure 2.7c, 2.7d). Micro moth communities showed a linear relationship with woody feature height, with communities

associated with lower woody features located towards the top of the plot whilst those associated with taller woody features are located towards the bottom of the plot. This relationship remained significant for farmland micro moths (Table S.2.8.). Macro moth communities found next to taller woody features are clustered in the middle of the plot whilst those associated with lower woody features are located towards the edges of plot, though the effect of woody feature height on farmland macro moth community composition was only marginally significant (Table S.2.8.). The effect of crop diversity index on community composition for macro moths was not significant and was only marginally significant for micro moths and farmland micro moths (Table S.2.8.).

2.4. Discussion

I found important effects of landscape configuration on understudied micro moths but not macro moths. Mixed farming indirectly benefitted micro moths by increasing woodland edge density, whilst woodland edge density also shaped micro moth community composition. However, this positive indirect effect was sometimes outweighed by a negative direct effect of mixed farming. At the local scale, woody feature height was also important, with taller woody features increasing micro moth abundance and woody feature height contributing to shaping both macro and micro moth communities.

2.4.1. Farming strategies

I found a direct negative effect of mixed farming in comparison to arable farming on micro moth species richness which is in agreement with (Fuentes-Montemayor et al., 2011) where higher micro moth abundance was found on arable farms compared with mixed farms. This could be because mixed farming

does not always lead to a reduction in intensive farming practices (Ryschawy et al., 2012). Indeed, I found no suggestion that mixed farms included in my study were using less synthetic fertiliser compared with arable farms (Table S.2.4.). In fact, pasture on mixed farms has the potential to be intensively managed similarly to arable fields, as it is often composed of high-energy grasses such as ryegrass, that requires higher levels of nitrogen input than a more diverse pasture. As well as the negative effects of fertiliser on moths, ryegrass monocultures provide very little food choice for grass-feeding moths. Furthermore, anthelmintics used for worming livestock are known to have a negative impact on non-target invertebrates (Scheffczyk et al., 2016) though more research is needed on the effects on Lepidoptera. Finally, cattle stocking rates used on the majority of mixed farms included in this study (> 2 Livestock units per hectare) are considered to be associated with higher inputs and productivity (Vertès et al., 2019). Grazing at lower stocking rates than those used on the farms in my study has been found to reduce moth abundance and diversity (Littlewood, 2008), though there is still a lack of research on the impacts of different grazing intensities on moths. Indeed, I found no evidence that pasture provides a more valuable habitat for moths than crop fields, which is different to Froidevaux et al. (2019) where arable fields were found to harbour lower macro moth diversity and abundance than grassland. This, in addition to the direct negative effect of mixed farming found in my SEMs, suggests that further research is needed to better understand pasture management strategies that are sympathetic to moths, whilst continuing to provide food to a growing human population.

Crop diversity had no effect on any of the moth groupings and was also not affected by farm type. Though previous studies have found higher insect diversity associated with higher crop diversity, most of these studied other insect families (Hass et al., 2018; Sirami et al., 2019). In addition, one study found that crop diversity only had a positive effect on biodiversity in landscapes where semi-natural areas were above 11% of the landscape (Aguilera et al.,

2020; Tassoni et al., 2024). Thus, crop diversity may not be influencing moths on my study sites, where semi-natural areas were low with a mean value of 1.5% for the 1000m scale (min 0%, max 10%). However, it is important to note that the definition of 'semi-natural' differed slightly between the two aforementioned studies as well as from my own.

2.4.2. Importance of landscape configuration for moths.

The most important landscape-scale feature for moths in this study was woodland edge density within 1000 m of traps. Though the positive effect of amount of woodland edge on both micro moths and macro moths could be due in part to an increase in woody plant-feeding species, interestingly this effect was still significant for farmland micro moths, with mean abundance increasing by 30% for every additional 22m per hectare of woodland edge. This positive influence of woodland on non-woodland Lepidoptera has been seen in previous studies for grassland macro moths (Kühne et al., 2022) and for grassland butterflies (Gaigher et al., 2024) but to my knowledge this study is the first to report the importance of woodland for micro moths that do not feed on woody plants. Woodland edges could provide sheltered areas for moths and may also be accompanied by other semi-natural or 'unfarmed' margins that are directly beneficial for moths (Fuentes-Montemayor et al., 2011; Merckx et al., 2012). In the landscapes studied here, woodland edge density also correlated negatively with the proportion of arable crop cover. Previous studies have shown that proportion of arable in the landscape correlates positively with fertiliser inputs (Roschewitz et al., 2005), as such landscapes with high woodland edge density are likely to be subjected to lower levels of nitrogen input. Furthermore, since moss-feeding micro moths were included in the farmland category (25% of total farmland micro moth abundance) it is possible that they could have influenced farmland micro moth response to

woodland edge density, as woodlands can offer damper habitats suitable for moss, with less disturbance than agricultural land.

Surprisingly, habitat diversity at the 1000 m scale significantly reduced micro moth abundance and farmland micro moth abundance. Since habitat diversity correlated negatively with the proportion of arable this may be indicative of reduced food availability for farmland micro moths that may be feeding on grass or crops, particularly since there was no impact on species richness or diversity. Alternatively, areas with higher habitat heterogeneity may contain more barriers to movement such as woodlands resulting in moth communities being more localised and less likely to encounter light traps.

In contrast to micro moths, landscape configuration (habitat diversity and woodland edge density) didn't explain any of the variation in macro moths which was mostly explained by temperature. It is important to note that multiple sites were trapped during warmer than average weather for North-East Scotland during mid-July (max temperature at sunset was 24 degrees Celsius). These high temperatures could potentially reduce or mask the effect of other environmental variables, particularly for macro moths that are generally more mobile than micro moths and may increase movement in response to warmer temperatures (Jonason et al., 2014). These differences between macro moth and micro moth response are seen elsewhere (Uhl et al., 2022) and results highlight the importance of studying both macro and micro moths.

I also acknowledge that my sampling design provides a snapshot of moth abundance, diversity and community composition on arable and mixed farms and responses could differ if sampling were to take place in spring or autumn. However, my paired design and sampling across 26 farms makes this a robust study in terms of comparing the effects of arable and mixed farms on moths at a time of year when a large number of moths are active.

2.4.3. Importance of local-scale woody features for moths.

The influence of woody feature height was not as important as that of woodland edge density in my SEMs. Farmland micro moth abundance, species richness and diversity increased with increasing woody feature height. Thus, taller woody features may be providing more sheltered areas and microclimates suitable for farmland micro moths in very open agricultural landscapes. Woody feature height also significantly affected macro and micro moth community composition. Although some of this effect could be due to the presence of woody-feeding species, this effect was still true for farmland micro moth community composition. Instead, the influence of woody feature height could be linked with the woody-plant species associated with different hedgerow or treeline heights. In my study, taller woody features were associated with different woody plant species such as conifers (*Picea* spp.) and sycamores (*Acer pseudoplatanus*) whilst lower woody features were associated with gorse (*Ulex europaeus*), dog-rose (*Rosa canina*) and hawthorn (*Crataegus monogyna*; Figure S.2.3.). Thus, differences in moth communities, abundance and diversity across a gradient of hedgerow/ treeline height may be driven by the woody plant species present rather than the height of the hedgerow/ treeline itself. In addition, a change in moth communities with height of the woody feature could also be due to different moth species preferring to fly at different heights (De Smedt et al., 2019). Thus, lower woody features may not be suitable for some macro moth species, flying at greater heights. I suggest that a range of structurally different woody features could help to increase macro and micro moth beta diversity in agricultural landscapes.

2.4.4. Conclusion

This study showed contrasting effects of mixed farming for moths, with benefits being indirectly mediated via woodland edge density. Thus, regardless

of farm type, increasing amounts of woodland edge on farmland will likely benefit micro moths, including farmland species that do not feed on woody features, whilst a variety of woody feature types (e.g. lower hedgerows and taller treelines) that support different moth communities may help to increase beta diversity of macro and micro moths across the farm, though this should be implemented in conjunction with reduced synthetic inputs to avoid the creation of ecological traps. More research is needed to understand why mixed farming may have direct negative effects on micro moths and to find livestock or pasture management practices that are beneficial for moths.

Data availability

Data are available online at the University of Stirling's DataSTORRE:

<http://hdl.handle.net/11667/244>

2.3. Acknowledgements

I would like to thank all land owners for allowing data collection to take place on their farms. I would like to further thank Dr Mark Young for identifying micro moths, sharing insightful knowledge on certain species and for advice on guild classification. Special thanks go to Charlotte Wood for assisting with both fieldwork and identifying moths in the lab. With further thanks to Patrick Cook and David Hood for their advice on building UV LED lights for moth trapping and to Dr Sarah Marley for providing helpful comments on the draft manuscript. This project was fully funded by Scotland's Rural College (SRUC).

Supplementary material Chapter 2

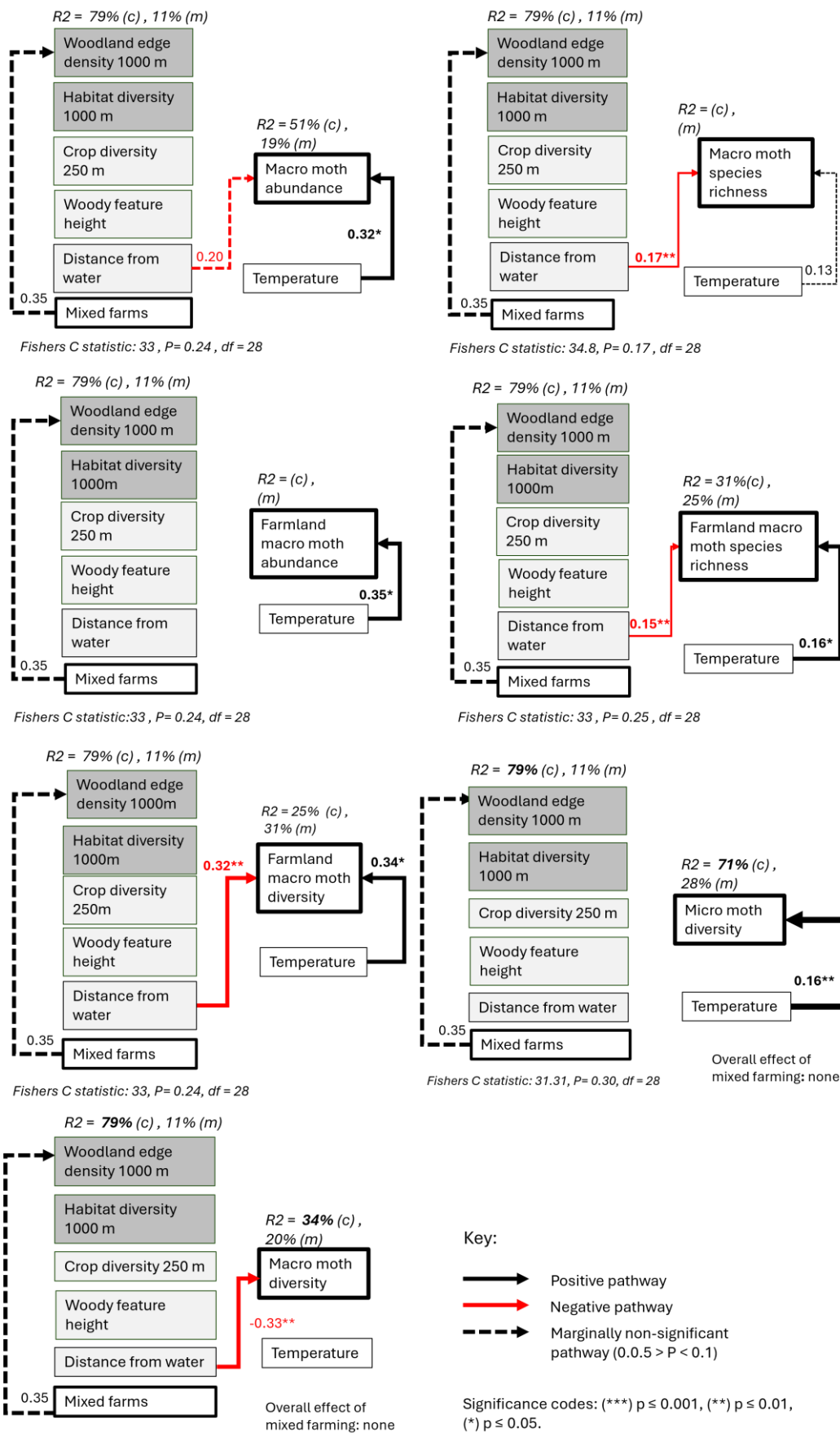


Figure S.2.1: Structural equation models where there was neither a direct or indirect effect of mixed farming on moths. Boxes represent variables included in each model. Standard estimates for each significant pathway are given next to the corresponding arrow. Dark grey boxes indicate a landscape-scale variable whilst light grey boxes are local-scale variables. Where arrows are absent this indicates no significant pathway between variables.

Table S.2.1 Table of crop categories used for calculating crop diversity index

Crop functional group	Crops included
Cereals	Barley, wheat, oats.
Legumes	Peas, beans.
Brassicas	Oilseed rape, cauliflower, Brussel sprouts, broccoli.
Root vegetables	Potatoes, carrots, suedes, turnips.
Grassland	Permanent pasture, temporary pasture and herbals leys (including clover – legume mixes).
Agri-envrionment scheme mix (AES)	Any seed mix sown as a part of agri-environment schemes such as bird mix, pollinator mix, wildflower mix etc.

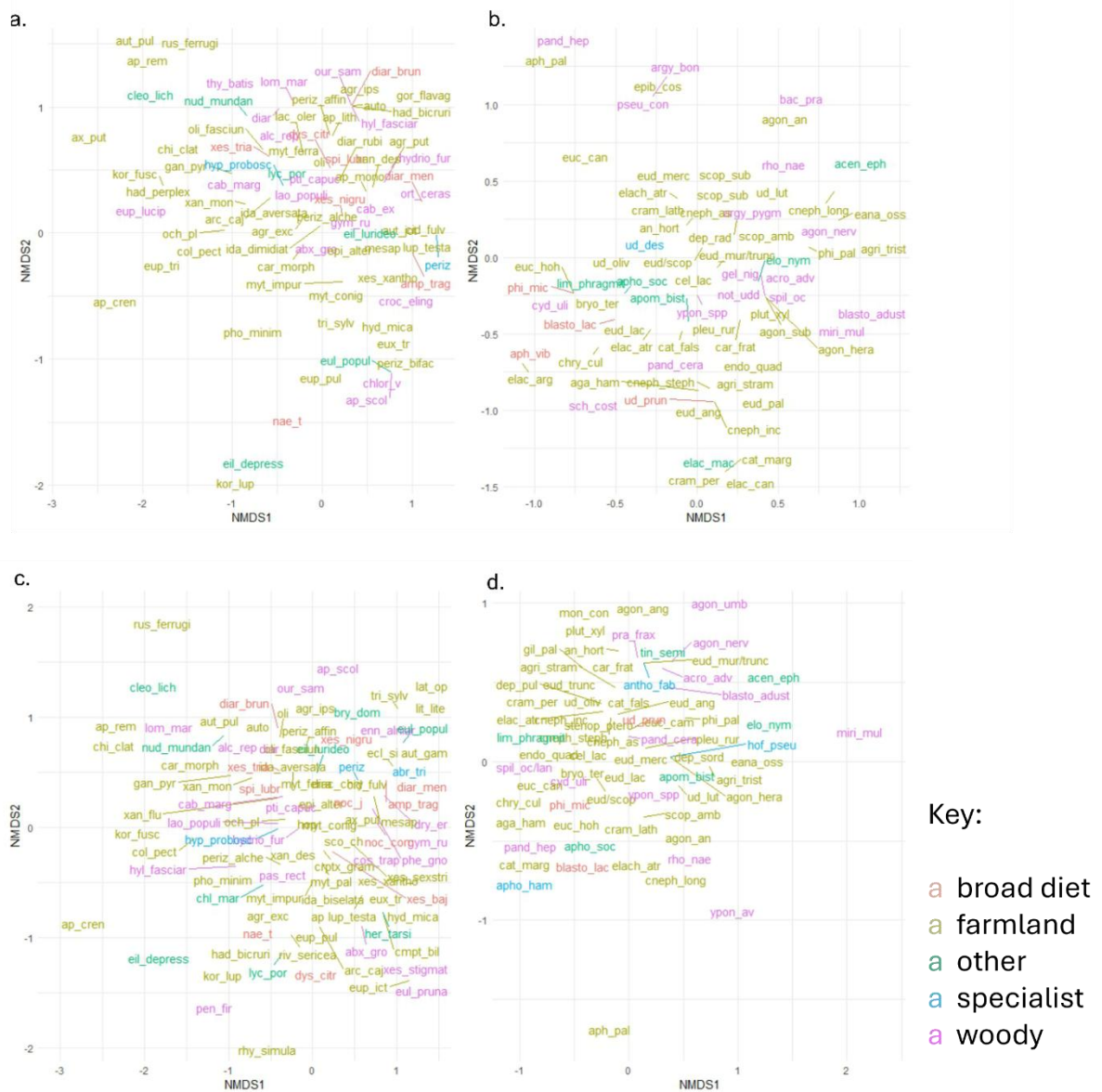


Figure S.2.2. NMDS ordination plots of dissimilarities between moth communities at the farm level for a. macro moths and b. micro moths; at the trap-level for a. macro moths and b. micro moths. Species names are abbreviated and can be found in full in Table S.2.7. Colours show different guilds according to larval food preferences.

Table S.2.2. Pearson correlation matrix of all variables considered for statistical analysis.

Variable	Latitude	Temperature	Woody feature height	Distance from water	Habitat diversity 250m	Habitat diversity 500m	Habitat diversity 1000m	Proportion grass 250m	Proportion grass 500m	Proportion grass 1000m	Proportion arable 250m	Proportion arable 500m	Proportion arable 1000m	Altitude	Woodland edge density 500m	Woodland edge density 1000m	Date	Crop diversity 250m
Latitude	1	-0.36	0.12	0.07	0.09	0.1	0.31	-0.13	-0.02	0.04	0	-0.14	-0.18	-0.12	-0.14	-0.27	0.25	0.08
Temperature	-0.36	1	-0.12	-0.2	0.21	0.24	0.21	0.21	0.18	0.31	-0.19	-0.22	-0.28	0.18	-0.001	0.15	0.16	-0.07
Woody feature height	0.12	-0.12	1	-0.12	0.13	0.04	-0.18	0.04	0.1	0.15	-0.13	-0.04	-0.02	0.07	0.27	0.07	-0.11	-0.15
Distance from water	0.07	-0.2	-0.12	1	-0.24	-0.17	0.03	-0.14	-0.09	0.03	0.13	0.06	-0.01	0.1	-0.22	-0.07	-0.24	0.12
Habitat diversity 250m	0.09	0.21	0.13	-0.24	1	0.72	0.24	0.15	0.18	0.22	-0.8	-0.64	-0.59	0.19	0.42	0.39	0.16	0
Habitat diversity 500m	0.1	0.24	0.04	-0.17	0.72	1	0.4	0.11	0.26	0.35	-0.67	-0.87	-0.79	0.3	0.54	0.45	0.17	-0.04
Habitat diversity 1000m	0.31	0.21	-0.18	0.03	0.24	0.4	1	-0.19	-0.15	-0.01	-0.19	-0.38	-0.53	0.3	-0.04	0.34	0.03	0.07
Proportion grass 250m	-0.13	0.21	0.04	-0.14	0.15	0.11	-0.19	1	0.79	0.39	-0.18	-0.14	0.01	0.12	0.12	-0.13	-0.14	-0.04
Proportion grass 500m	-0.02	0.18	0.1	-0.09	0.18	0.26	-0.15	0.79	1	0.71	-0.22	-0.35	-0.23	0.01	0.17	-0.05	-0.11	-0.04
Proportion grass 1000m	0.04	0.31	0.15	0.03	0.22	0.35	-0.01	0.39	0.71	1	-0.35	-0.47	-0.47	0.1	0.21	0.12	-0.11	-0.02
Proportion arable 250m	0	-0.19	-0.13	0.13	-0.8	-0.67	-0.19	-0.18	-0.22	-0.35	1	0.82	0.65	-0.3	-0.56	-0.4	0.01	0.11
Proportion arable 500m	-0.14	-0.22	-0.04	0.06	-0.64	-0.87	-0.38	-0.14	-0.35	-0.47	0.82	1	0.84	-0.33	-0.58	-0.39	-0.02	0.08
Proportion arable 1000m	-0.18	-0.28	-0.02	-0.01	-0.59	-0.79	-0.53	0.01	-0.23	-0.47	0.65	0.84	1	-0.4	-0.44	-0.59	-0.12	-0.07
Altitude	-0.12	0.18	0.07	0.1	0.19	0.3	0.3	0.12	0.01	0.1	-0.3	-0.33	-0.4	1	0.33	0.24	-0.21	0.09
Woodland edge density 500m	-0.14	0.001	0.27	-0.22	0.42	0.54	-0.04	0.12	0.17	0.21	-0.56	-0.58	-0.44	0.33	1	0.47	0.02	-0.11
Woodland edge density 1000m	-0.27	0.15	0.07	-0.07	0.39	0.45	0.34	-0.13	-0.05	0.12	-0.4	-0.39	-0.59	0.24	0.47	1	-0.1	0.09
Date	0.25	0.16	-0.11	-0.24	0.16	0.17	0.03	-0.14	-0.11	-0.11	0.01	-0.02	-0.12	-0.21	0.02	-0.1	1	-0.17
Crop diversity 250m	0.08	-0.07	-0.15	0.12	0	-0.04	0.07	-0.04	-0.04	-0.02	0.11	0.08	-0.07	0.09	-0.11	0.09	-0.17	1

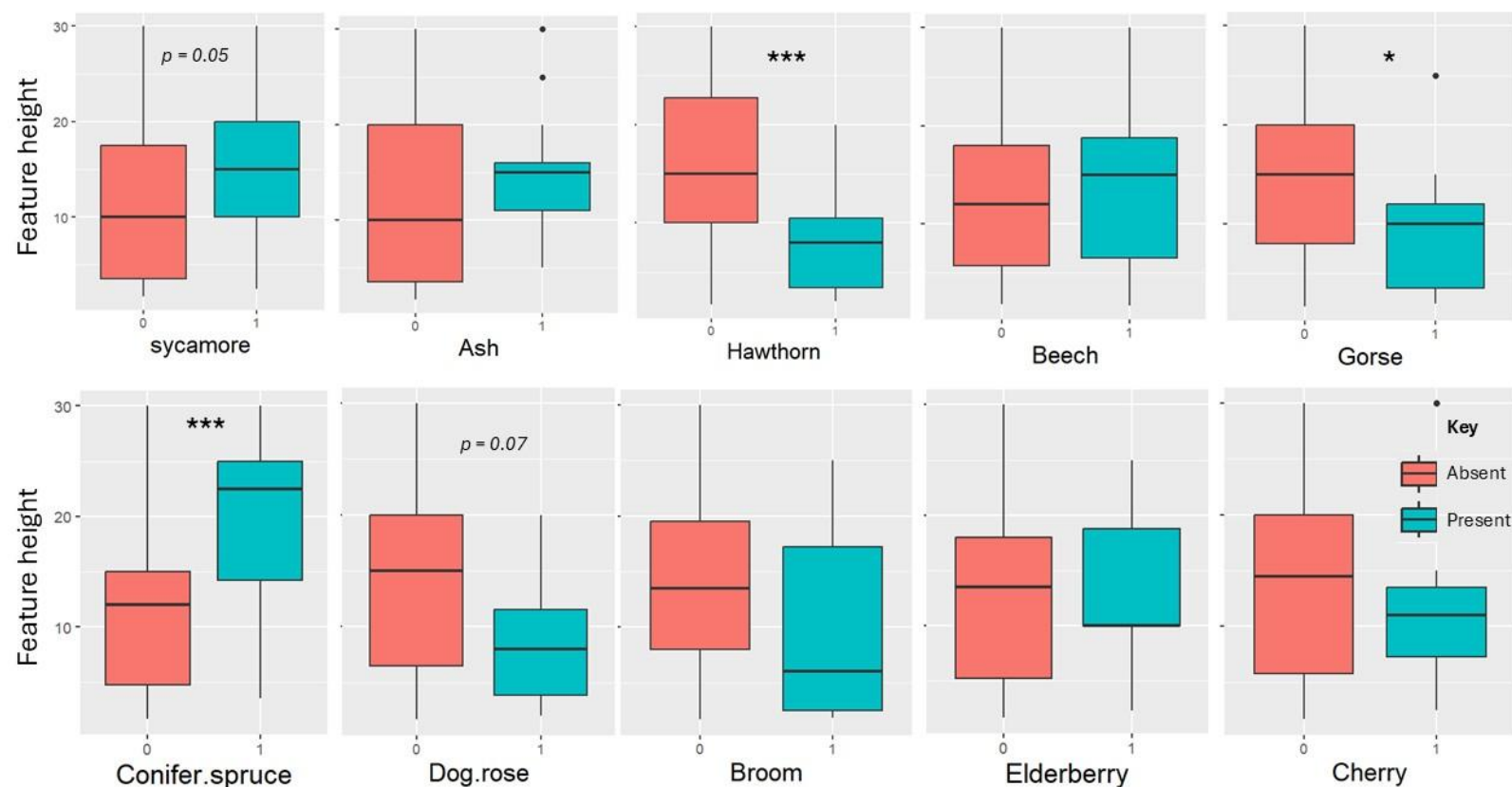


Figure S.2.3. Boxplots showing differences in hedgerow/ treeline composition (in terms of presence of different woody plant species) associated with estimated hedgerow/ treeline height (e.g. 'woody feature height'). Taller hedgerows/ treelines were significantly associated with the presence of Coniferous trees and marginally non-significantly associated with the presence of Sycamore. Lower hedgerows were significantly associated with the presence of Gorse and hawthorn and marginally non-significantly associated with dog rose. Significance was determined using Wilcoxon unpaired tests in R.

Table S.2.3. R squared values (for normally distributed data) and pseudo r squared values (for count data) that were used for landscape variable selection.

Moth group	Distribution	Habitat diversity 1000m	Proportion of arable 250m	Proportion of arable 500m	Proportion of arable 1000m	Proportion of grass 250m	Proportion of grass 500m	Proportion of grass 1000m	WED 1000m
Macro moth abundance	Negative binomial	0.0001	<0.0001	<0.0001	<0.0001	0.02	0.01	<0.0001	0.01
Macro moth species richness	Negative binomial	0.0003	0.02	0.01	0.01	0.09	0.02	0.006	0.025
Macro moth diversity	Gaussian	0.0008	0.014	0.005	0.009	0.083	0.015	0.006	0.052
Micro moth abundance	Negative binomial	0.019	0.1	0.02	0.03	<0.0001	<0.0001	0.014	0.041
Micro moth species richness	Negative binomial	0.004	0.04	0.02	0.02	<0.0001	<0.0001	<0.0001	0.073
Micro moth diversity	Gaussian	0.0001	0.092	0.042	0.044	0.0017	<0.0001	0.007	0.034
Farmland macro moth abundance	Negative binomial	0.005	<0.0001	<0.0001	<0.0001	0.01	<0.0001	<0.0001	0.013
Farmland macro moth richness	Negative binomial	0.004	0.04	0.03	0.05	0.09	0.04	0.034	0.044
Farmland macro moth diversity	Gaussian	0.004	0.019	0.012	0.025	0.09	0.024	0.02	0.113
Farmland micro moth abundance	Negative binomial	0.0001	0.06	0.02	0.06	0.01	<0.0001	0.048	0.055
Farmland micro moth richness	Negative binomial	0.0002	0.11	0.07	0.06	0.02	0.01	0.019	0.038
Farmland micro moth diversity	Gaussian	0.003	0.11	0.044	0.053	0.015	0.003	0.021	0.018

Table S.2.4.: Summary of synthetic nitrogen fertiliser applications for the year of 2022 for mixed and arable farms used in this study (where this information was provided).

	Mean N Kg ⁻¹ Ha ⁻¹ for winter wheat	Mean N Kg ⁻¹ Ha ⁻¹ for spring barley
Arable (n = 6)	142.4	125.6
Mixed (n = 5)	(min = 60, max = 200) 167.8	(min = 73, max = 150) 143.1
	(min = 0, max = 297)	(min = 0, max = 297)

Table S.2.5: Model estimates for all pathways and correlated errors (indicated by '~~') included in all SEMs.

<i>Response variable</i>	<i>Predictor variable</i>	<i>Estimate</i>	<i>Standard Error</i>	<i>DF</i>	<i>P.Value</i>	<i>Standardised estimate</i>
<i>Farmland macro moth abundance (log)</i>	Farm type (mixed)	0.0894	0.1514	21.6983	0.5628	0.0925
<i>Farmland macro moth abundance (log)</i>	Temperature^a	0.3494	0.153	20.267	0.034	0.3591
<i>Farmland macro moth abundance (log)</i>	Crop diversity 250 m	0.0199	0.1	59.8697	0.8468	0.0204
<i>Farmland macro moth abundance (log)</i>	Woodland edge density 1000 m	-0.172	0.1425	43.7909	0.2497	-0.1768
<i>Farmland macro moth abundance (log)</i>	Distance from water	-0.197	0.1	58.5593	0.059	-0.2025
<i>Farmland macro moth abundance (log)</i>	Woody feature height	-0.1471	0.1108	63.5884	0.2018	-0.1511
<i>Farmland macro moth abundance (log)</i>	Habitat diversity 1000 m	-0.0603	0.1467	29.5148	0.6911	-0.0619

<i>Crop diversity 250 m</i>	Farm type (mixed)	-0.0298	0.1301	23.456	0.8213	-0.03
<i>Woodland edge density 1000 m</i>	Farm type (mixed)	0.3463	0.1747	23.9878	0.0591	0.3486
<i>Woody feature height</i>	Farm type (mixed)	-0.1806	0.1425	23.7356	0.2179	-0.1818
<i>Habitat diversity 1000 m</i>	Farm type (mixed)	0.167	0.1912	23.9985	0.3909	0.1681
~~ Habitat diversity 500 m	~~Woodland edge density 1000 m	0.2738	-	72	0.0104	0.2738
<i>Farmland macro moth diversity</i>	Farm type (mixed)	0.0417	0.0597	19.4585	0.4961	0.0876
Farmland macro moth diversity	Temperature	0.1624	0.0591	16.6083	0.0147	0.3386
<i>Farmland macro moth diversity</i>	Crop diversity 250 m	0.0625	0.0528	63.4194	0.2556	0.1304
<i>Farmland macro moth diversity</i>	Woodland edge density 1000 m	-0.0010	0.0623	28.7839	0.9880	-0.0020
Farmland macro moth diversity	Distance from water	-0.1518	0.0531	63.6255	0.0075	-0.3166
<i>Farmland macro moth diversity</i>	Woody feature height	-0.0230	0.0561	56.7202	0.6944	-0.0479
<i>Farmland macro moth diversity</i>	Habitat diversity 1000 m	-0.0191	0.0602	21.7227	0.7575	-0.0399
<i>Crop diversity 250 m</i>	Farm type (mixed)	-0.0298	0.1301	23.456	0.8213	-0.03
<i>Woodland edge density 1000 m</i>	Farm type (mixed)	0.3463	0.1747	23.9878	0.0591	0.3486
<i>Woody feature height</i>	Farm type (mixed)	-0.1806	0.1425	23.7356	0.2179	-0.1818
<i>Habitat diversity 1000 m</i>	Farm type (mixed)	0.167	0.1912	23.9985	0.3909	0.1681

<i>Farmland macro moth species richness (log)</i>	Farm type (mixed)	0.0417	0.0597	19.4585	0.4961	0.0876
<i>Farmland macro moth species richness (log)</i>	Temperature	0.1624	0.0591	16.6083	0.0147	0.3386
<i>Farmland macro moth species richness (log)</i>	Crop diversity 250 m	0.0625	0.0528	63.4194	0.2556	0.1304
<i>Farmland macro moth species richness (log)</i>	Woodland edge density 1000 m	-0.001	0.0623	28.7839	0.988	-0.002
<i>Farmland macro moth species richness (log)</i>	Distance from water	-0.1518	0.0531	63.6255	0.0075	-0.3166
<i>Farmland macro moth species richness (log)</i>	Woody feature height	-0.023	0.0561	56.7202	0.6944	-0.0479
<i>Farmland macro moth species richness (log)</i>	Habitat diversity 1000 m	-0.0191	0.0602	21.7227	0.7575	-0.0399
<i>Crop diversity 250 m</i>	Farm type (mixed)	-0.0298	0.1301	23.456	0.8213	-0.03
<i>Woodland edge density 1000 m</i>	Farm type (mixed)	0.3463	0.1747	23.9878	0.0591	0.3486
<i>Woody feature height</i>	Farm type (mixed)	-0.1806	0.1425	23.7356	0.2179	-0.1818
<i>Habitat diversity 1000 m</i>	Farm type (mixed)	0.167	0.1912	23.9985	0.3909	0.1681
<i>Farmland micro moth abundance (log)</i>	Farm type (mixed)	-0.1311	0.1313	22.3992	0.3307	-0.1377
<i>Farmland micro moth abundance (log)</i>	Temperature	0.6281	0.1334	21.1706	1e-04	0.6552
<i>Farmland micro moth abundance (log)</i>	Crop diversity 250 m	0.1037	0.0756	56.049	0.1838	0.1082
<i>Farmland micro moth abundance (log)</i>	Woodland edge density 1000 m	0.2803	0.1158	52.1782	0.0235	0.2924
<i>Farmland micro moth abundance (log)</i>	Distance from water	0.0793	0.0754	54.5091	0.3058	0.0827

Farmland micro moth abundance (log)	Woody feature height	0.183	0.0849	60.9427	0.0396	0.1909
<i>Farmland micro moth abundance (log)</i>	Habitat diversity 1000 m	-0.2318	0.1234	34.4673	0.0763	-0.2418
<i>Crop diversity 250 m</i>	Farm type (mixed)	-0.0298	0.1301	23.456	0.8213	-0.03
<i>Woodland edge density 1000 m</i>	Farm type (mixed)	0.3463	0.1747	23.9878	0.0591	0.3486
<i>Woody feature height</i>	Farm type (mixed)	-0.1806	0.1425	23.7356	0.2179	-0.1818
<i>Habitat diversity 1000 m</i>	Farm type (mixed)	0.167	0.1912	23.9985	0.3909	0.1681
<i>Farmland micro moth diversity (log)</i>	Farm type (mixed)	-0.0393	0.0885	22.7728	0.6621	-0.0749
<i>Farmland micro moth diversity (log)</i>	Temperature	0.2709	0.0901	21.6346	8.9716	0.5127
<i>Farmland micro moth diversity (log)</i>	Crop diversity 250 m	0.0639	0.0464	53.6449	0.1809	0.1209
<i>Farmland micro moth diversity (log)</i>	Woodland edge density 1000 m	0.1104	0.0742	57.3891	0.1565	0.2090
<i>Farmland micro moth diversity (log)</i>	Distance from water	0.0184	0.0461	52.1052	0.6952	0.0349
<i>Farmland micro moth diversity (log)</i>	Woody feature height	0.0936	0.0525	58.5459	0.0859	0.1722
<i>Farmland micro moth diversity (log)</i>	Habitat diversity 1000 m	-0.1018	0.0810	38.5016	0.2303	-0.1927
<i>Crop diversity 250 m</i>	Farm type (mixed)	-0.0298	0.1301	23.456	0.8213	-0.03
<i>Woodland edge density 1000 m</i>	Farm type (mixed)	0.3463	0.1747	23.9878	0.0591	0.3486
<i>Woody feature height</i>	Farm type (mixed)	-0.1806	0.1425	23.7356	0.2179	-0.1818

<i>Habitat diversity 1000 m</i>	Farm type (mixed)	0.167	0.1912	23.9985	0.3909	0.1681
<i>Farmland micro moth species richness (log)</i>	Farm type (mixed)	-0.0393	0.0885	22.7728	0.6621	-0.0749
<i>Farmland micro moth species richness (log)</i>	Temperature	0.2709	0.0901	21.6346	0.0067	0.5127
<i>Farmland micro moth species richness (log)</i>	Crop diversity 250 m	0.0639	0.0464	53.6449	0.1809	0.1209
<i>Farmland micro moth species richness (log)</i>	Woodland edge density 1000 m	0.1104	0.0742	57.3891	0.1565	0.209
<i>Farmland micro moth species richness (log)</i>	Distance from water	0.0184	0.0461	52.1052	0.6952	0.0349
<i>Farmland micro moth species richness (log)</i>	Woody feature height	0.0936	0.0525	58.5459	0.0859	0.1772
<i>Farmland micro moth species richness (log)</i>	Habitat diversity 1000 m	-0.1018	0.081	38.5016	0.2303	-0.1927
<i>Crop diversity 250 m</i>	Farm type (mixed)	-0.0298	0.1301	23.456	0.8213	-0.03
<i>Woodland edge density 1000 m</i>	Farm type (mixed)	0.3463	0.1747	23.9878	0.0591	0.3486
<i>Woody feature height</i>	Farm type (mixed)	-0.1806	0.1425	23.7356	0.2179	-0.1818
<i>Habitat diversity 1000 m</i>	Farm type (mixed)	0.167	0.1912	23.9985	0.3909	0.1681
<i>Macro moth abundance (log)</i>	Farm type (mixed)	0.0348	0.1465	21.5968	0.8155	0.0375
<i>Macro moth abundance (log)</i>	Temperature	0.3184	0.1479	20.129	0.0445	0.3414
<i>Macro moth abundance (log)</i>	Crop diversity 250 m	-0.0246	0.0984	60.3411	0.8081	-0.0264
<i>Macro moth abundance (log)</i>	Woodland edge density 1000 m	-0.1132	0.1388	42.7573	0.4351	-0.1214

<i>Macro moth abundance (log)</i>	Distance from water	-0.2005	0.0985	59.0879	0.0512	-0.215
<i>Macro moth abundance (log)</i>	Woody feature height	-0.1081	0.1088	63.7697	0.3382	-0.1159
<i>Macro moth abundance (log)</i>	Habitat diversity 1000 m	-0.1091	0.1423	28.9654	0.4599	-0.117
<i>Crop diversity 250 m</i>	Farm type (mixed)	-0.0298	0.1301	23.456	0.8213	-0.03
<i>Woodland edge density 1000 m</i>	Farm type (mixed)	0.3463	0.1747	23.9878	0.0591	0.3486
<i>Woody feature height</i>	Farm type (mixed)	-0.1806	0.1425	23.7356	0.2179	-0.1818
<i>Habitat diversity 1000 m</i>	Farm type (mixed)	0.167	0.1912	23.9985	0.3909	0.1681
~~ Habitat diversity 500 m	~~Woodland edge density 1000 m	0.2738	-	72	0.0104	0.2738
<i>Macro moth diversity</i>	Farm type (mixed)	0.0417	0.0597	19.4585	0.4961	0.0876
Macro moth diversity	Temperature	0.1624	0.0591	16.6083	0.0147	0.3386
<i>Macro moth diversity</i>	Crop diversity 250 m	0.0625	0.0528	63.4194	0.2556	0.1304
<i>Macro moth diversity</i>	Woodland edge density 1000 m	-0.0010	0.0623	28.7839	0.9880	-0.0020
Macro moth diversity	Distance from water	-0.1518	0.0531	63.6255	0.0075	-0.3166
<i>Macro moth diversity</i>	Woody feature height	-0.0230	0.0561	56.7202	0.6944	-0.0479
<i>Macro moth diversity</i>	Habitat diversity 1000 m	-0.0191	0.0602	21.7227	0.7575	-0.0399
<i>Crop diversity 250 m</i>	Farm type (mixed)	-0.0298	0.1301	23.456	0.8213	-0.03

Woodland edge density 1000 m	Farm type (mixed)	0.3463	0.1747	23.9878	0.0591	0.3486
Woody feature height	Farm type (mixed)	-0.1806	0.1425	23.7356	0.2179	-0.1818
Habitat diversity 1000 m	Farm type (mixed)	0.167	0.1912	23.9985	0.3909	0.1681
Macro moth species richness (log)	Farm type (mixed)	0.0123	0.0718	20.2908	0.8666	0.024
Macro moth species richness (log)	Temperature	0.1315	0.0717	18.1289	0.085	0.2552
Macro moth species richness (log)	Crop diversity 250 m	0.0139	0.0579	63.9193	0.8167	0.0269
Macro moth species richness (log)	Woodland edge density 1000 m	0.0321	0.0728	32.8007	0.6712	0.0623
Macro moth species richness (log)	Habitat diversity 1000 m	-0.0517	0.0717	23.8556	0.4855	-0.1003
Macro moth species richness (log)	Distance from water	-0.1726	0.0582	63.6992	0.0054	-0.3348
Macro moth species richness (log)	Woody feature height	0.0041	0.0624	61.5797	0.9498	0.0079
Crop diversity 250 m	Farm type (mixed)	-0.0298	0.1301	23.456	0.8213	-0.03
Woodland edge density 1000 m	Farm type (mixed)	0.3463	0.1747	23.9878	0.0591	0.3486
Woody feature height	Farm type (mixed)	-0.1806	0.1425	23.7356	0.2179	-0.1818
Habitat diversity 1000 m	Farm type (mixed)	0.167	0.1912	23.9985	0.3909	0.1681
Micro moth abundance (log)	Farm type (mixed)	-0.1449	0.1353	22.5928	0.2975	-0.1594
Micro moth abundance (log)	Temperature	0.5594	0.1377	21.411	6e-04	0.6113

<i>Micro moth abundance (log)</i>	Crop diversity 250 m	0.0241	0.0744	54.836	0.7517	0.0263
<i>Micro moth abundance (log)</i>	Woodland edge density 1000 m	0.2728	0.1165	54.8452	0.0279	0.2982
<i>Micro moth abundance (log)</i>	Distance from water	-0.0137	0.0741	53.2854	0.8564	-0.015
<i>Micro moth abundance (log)</i>	Woody feature height	0.126	0.0839	59.7893	0.1472	0.1377
<i>Micro moth abundance (log)</i>	Habitat diversity 1000 m	-0.3251	0.1257	36.3778	0.0165	-0.3553
<i>Crop diversity 250 m</i>	Farm type (mixed)	-0.0298	0.1301	23.456	0.8213	-0.03
<i>Woodland edge density 1000 m</i>	Farm type (mixed)	0.3463	0.1747	23.9878	0.0591	0.3486
<i>Woody feature height</i>	Farm type (mixed)	-0.1806	0.1425	23.7356	0.2179	-0.1818
<i>Habitat diversity 1000 m</i>	Farm type (mixed)	0.167	0.1912	23.9985	0.3909	0.1681
<i>Micro moth diversity</i>	Farm type (mixed)	-0.0556	0.0937	22.7119	0.5608	-0.1000
<i>Micro moth diversity</i>	Woodland edge density 1000 m	0.1280	0.0793	56.5270	0.1252	0.2288
<i>Micro moth diversity</i>	Woody feature height	0.0724	0.0565	58.9856	0.2149	0.1293
<i>Micro moth diversity</i>	Distance from water	>0.00001	0.0497	52.5094	0.9993	0.0001
<i>Micro moth diversity</i>	Habitat diversity 1000 m	-0.0948	0.0863	37.7388	1.1372	-0.1694
<i>Micro moth diversity</i>	Temperature	0.2914	0.0954	21.5588	0.0061	0.5207
<i>Micro moth diversity</i>	Crop diversity 250 m	0.0264	0.0500	54.0550	0.6048	0.0473

<i>Crop diversity 250 m</i>	Farm type (mixed)	-0.0298	0.1301	23.456	0.8213	-0.03
<i>Woodland edge density 1000 m</i>	Farm type (mixed)	0.3463	0.1747	23.9878	0.0591	0.3486
<i>Woody feature height</i>	Farm type (mixed)	-0.1806	0.1425	23.7356	0.2179	-0.1818
<i>Habitat diversity 1000 m</i>	Farm type (mixed)	0.167	0.1912	23.9985	0.3909	0.1681
<i>Micro moth species richness (log)</i>	Farm type (mixed)	-0.144	0.0704	19.1849	0.0564	-0.2563
<i>Micro moth species richness (log)</i>	Woodland edge density 1000 m	0.1928	0.074	27.7326	0.017	0.341
<i>Micro moth species richness (log)</i>	Woody feature height	-0.0758	0.0675	54.8153	0.2845	-0.134
<i>Micro moth species richness (log)</i>	Distance from water	0.0389	0.0643	63.0209	0.5616	0.0688
<i>Micro moth species richness (log)</i>	Temperature	0.1858	0.0694	16.0654	0.0174	0.3286
<i>Micro moth species richness (log)</i>	Habitat diversity 1000 m	-0.0556	0.0711	21.1395	0.4493	-0.0984
<i>Micro moth species richness (log)</i>	Crop diversity 250 m	-0.0313	0.0639	62.8128	0.6368	-0.0554
<i>Crop diversity 250 m</i>	Farm type (mixed)	-0.0298	0.1301	23.456	0.8213	-0.03
<i>Woodland edge density 1000 m</i>	Farm type (mixed)	0.3463	0.1747	23.9878	0.0591	0.3486
<i>Woody feature height</i>	Farm type (mixed)	-0.1806	0.1425	23.7356	0.2179	-0.1818
<i>Habitat diversity 1000 m</i>	Farm type (mixed)	0.167	0.1912	23.9985	0.3909	0.1681

^aSignificant pathways are shown in bold

Table S.2.6. Species scientific names, abbreviations used in NMDS plots and total number of individuals per species.

<i>Scientific name</i>	<i>Abbreviation for NMDS plots</i>	<i>number of individuals</i>	<i>Percentage total catch</i>	<i>Guild</i>	<i>Macro/ micro</i>
<i>Noctua pronuba</i>	noc.pro	1846	19.96	Farmland	Macro
<i>Mesapamea</i> spp.	mesap	1310	14.16	Farmland	Macro
<i>Mythimna impura</i>	myt.impur	720	7.78	Farmland	Macro
<i>Agriphila straminella</i>	agri.stram	508	5.49	Farmland	Micro
<i>Blastobasis adustella</i>	blasto.adust	273	2.95	Woody	Micro
<i>Eudonia lacustrata</i>	eud.lac	234	2.53	Farmland	Micro
<i>Chrysoteuchia culmella</i>	chry.cul	209	2.26	Farmland	Micro
<i>Apamea monoglypha</i>	ap.mono	189	2.04	Farmland	Macro
<i>Udea lutealis</i>	ud.lut	162	1.75	Farmland	Micro
<i>Noctua janthe</i>	noc.j	161	1.74	Broad diet	Macro
<i>Agriphila tristella</i>	agri.trist	152	1.64	Farmland	Micro
<i>Xestia baja</i>	xes.baj	144	1.56	Broad diet	Macro
<i>Luperina testacea</i>	lup.testa	137	1.48	Farmland	Macro
<i>Xestia triangulum</i>	xes.tria	115	1.24	Broad diet	Macro
<i>Scoparia ambigualis</i>	scop.amb	111	1.2	Farmland	Micro
<i>Scotopteryx chenopodiata</i>	sco.ch	110	1.19	Farmland	Macro
<i>Cnephasia asseclana</i>	cneph.as	108	1.17	Farmland	Micro
<i>Xestia sexstrigata</i>	xes.sexstri	106	1.15	Farmland	Macro
<i>Alcis repandata</i>	alc.rep	104	1.12	Woody	Macro
<i>Mythimna pallens</i>	myt.pal	103	1.11	Farmland	Macro
<i>Gandaritis pyraliata</i>	gan.pyr	95	1.03	Farmland	Macro
<i>Nudaria mundana</i>	nud.mundan	83	0.9	Other	Macro
<i>Cerapteryx graminis</i>	crptx.gram	75	0.81	Farmland	Macro
<i>Acentria ephemerella</i>	acen.eph	73	0.79	Other	Micro
<i>Noctua comes</i>	noc.com	72	0.78	Broad diet	Macro
<i>Mythimna ferrago</i>	myt.ferra	71	0.77	Farmland	Macro
<i>Celypha lacunana</i>	cel.lac	69	0.75	Farmland	Micro
<i>Cnephasia</i> spp.	cneph	66	0.71	Farmland	Micro
<i>Korscheltellus fusconebulosa</i>	kor.fusc	66	0.71	Farmland	Macro
<i>Hypena proboscidalis</i>	hyp.probosc	63	0.68	Specialist	Macro
<i>Hydriomena furcata</i>	hydrio.fur	62	0.67	Woody	Macro
<i>Amphipyra tragopoginis</i>	amp.trag	58	0.63	Broad diet	Macro
<i>Xanthorhoe montanata</i>	xan.mon	58	0.63	Farmland	Macro
<i>Diarsia rubi</i>	diar.rubi	57	0.62	Farmland	Macro
<i>Idaea aversata</i>	ida.aversata	53	0.57	Farmland	Macro
<i>Hoplodrina</i> spp	hop	52	0.56	Farmland	Macro

<i>Xestia xanthographa</i>	xes.xantho	44	0.48	Farmland	Macro
<i>Eana osseana</i>	eana.oss	42	0.45	Farmland	Micro
<i>Epirrhoe alternata</i>	epi.alter	41	0.44	Farmland	Macro
<i>Agapeta Hamana</i>	aga.ham	38	0.41	Farmland	Micro
<i>Agrotis exclamation</i>	agr.exc	38	0.41	Farmland	Macro
<i>Eilema lurideola</i>	eil.lurideo	38	0.41	Other	Macro
<i>Diachrysia chrysis</i>	diac.chry	37	0.4	Farmland	Macro
<i>Cosmia trapezina</i>	cos.trap	35	0.38	Woody	Macro
<i>Oligia fasciuncula</i>	oli.fasciun	34	0.37	Farmland	Macro
<i>Catoptria falsella</i>	cat.fals	33	0.36	Farmland	Micro
<i>Hydraecia micacea</i>	hyd.mica	31	0.34	Farmland	Macro
<i>Idaea biselata</i>	ida.biselata	30	0.32	Farmland	Macro
<i>Eudonia/Scoparia</i>	eud/scop	29	0.31	Farmland	Micro
<i>Pleuroptya ruralis</i>	pleu.rur	27	0.29	Farmland	Micro
<i>Eudonia mercurella</i>	eud.merc	25	0.27	Farmland	Micro
<i>Lacanobia oleracea</i>	lac.oler	23	0.25	Farmland	Macro
<i>Diarsia mendica</i>	diar.men	22	0.24	Broad diet	Macro
<i>Perizoma alchemillata</i>	periz.alche	22	0.24	Farmland	Macro
<i>Bryotropha terrella</i>	bryo.ter	21	0.23	Farmland	Micro
<i>Lycophotia porphyrea</i>	lyc.por	20	0.22	Other	Macro
<i>Udea olivalis</i>	ud.oliv	20	0.22	Farmland	Micro
<i>Campaea margaritaria</i>	cab.marg	19	0.21	Woody	Macro
<i>Plutella xylostella</i>	plut.xyl	19	0.21	Farmland	Micro
<i>Cnephasia stephansiana</i>	cneph.steph	18	0.19	Farmland	Micro
<i>Caryocolum fraternella</i>	car.frat	17	0.18	Farmland	Micro
<i>Cnephasia longana</i>	cneph.long	17	0.18	Farmland	Micro
<i>Eucosma cana</i>	euc.can	17	0.18	Farmland	Micro
<i>Scoparia subfusca</i>	scop.sub	17	0.18	Farmland	Micro
<i>Apamea lithoxylaea</i>	ap.lith	16	0.17	Farmland	Macro
<i>Pandemis cerasana</i>	pand.cera	16	0.17	Woody	Micro
<i>Mythimna conigera</i>	myt.conig	15	0.16	Farmland	Macro
<i>Rivula sericealis</i>	riv.sericea	15	0.16	Farmland	Macro
<i>Cnephasia incertana</i>	cneph.inc	14	0.15	Farmland	Micro
<i>Xanthorhoe designata</i>	xan.des	14	0.15	Farmland	Macro
<i>Crocallis elinguaris</i>	croc.eling	13	0.14	Woody	Macro
<i>Colostygia pectinataria</i>	col.pect	11	0.12	Farmland	Macro
<i>Diarsia brunnea</i>	diar.brun	11	0.12	Broad diet	Macro
<i>Elachista atricomella</i>	elac.atr	11	0.12	Farmland	Micro
<i>Laothoe populi</i>	lao.populi	11	0.12	Woody	Macro
<i>Oligia spp</i>	oli	11	0.12	Farmland	Macro
<i>Photodes minima</i>	pho.minim	11	0.12	Farmland	Macro
<i>Ptilodon capucina</i>	pti.capuc	11	0.12	Woody	Macro
<i>Crambus perlella</i>	cram.per	10	0.11	Farmland	Micro

<i>Endothenia quadrimaculana</i>	endo.quad	10	0.11	Farmland	Micro
<i>Mesotype didymata</i>	mes.didym	10	0.11	Farmland	Macro
<i>Perizoma affinitata</i>	periz.affin	10	0.11	Farmland	Macro
<i>Xanthorhoe fluctuata</i>	xan.flu	10	0.11	Farmland	Macro
<i>Yponomeuta</i> spp.	ypom.spp	10	0.11	Woody	Micro
<i>Chiasmia clathrata</i>	chi.clat	9	0.1	Farmland	Macro
<i>Ochropleura plecta</i>	och.pl	9	0.1	Farmland	Macro
<i>Abrostola tripartita</i>	abr.tri	8	0.09	Specialist	Macro
<i>Agonopterix nervosa</i>	agon.nerv	8	0.09	Woody	Micro
<i>Autographa jota</i>	aut.jot	8	0.09	Farmland	Macro
<i>Hadena bicruris</i>	had.bicruri	8	0.09	Farmland	Macro
<i>Acrobasis advenella</i>	acro.adv	7	0.08	Woody	Micro
<i>Aphomia sociella</i>	apho.soc	7	0.08	Other	Micro
<i>Autographa gamma</i>	aut.gam	7	0.08	Farmland	Macro
<i>Triodia sylvina</i>	tri.sylv	7	0.08	Farmland	Macro
<i>Abraxas grossulariata</i>	abx.gro	6	0.06	Woody	Macro
<i>Arctia caja</i>	arc.caj	6	0.06	Farmland	Macro
<i>Blastobasis lactricdella</i>	blasto.lac	6	0.06	Broad diet	Micro
<i>Dysstroma citrata</i>	dys.citr	6	0.06	Broad diet	Macro
<i>Ecliptopera silaceata</i>	ecl.si	6	0.06	Farmland	Macro
<i>Eudonia pallida</i>	eud.pal	6	0.06	Farmland	Micro
<i>Eudonia trunciolella</i>	eud.trunc	6	0.06	Farmland	Micro
<i>Litoligia literosa</i>	lit.lite	6	0.06	Farmland	Macro
<i>Prays fraxinella</i>	pra.frax	6	0.06	Woody	Micro
<i>Xestia c-nigrum</i>	xes.nigru	6	0.06	Broad diet	Macro
<i>Agonopterix heracliata</i>	agon.hera	5	0.05	Farmland	Micro
<i>Anania hortulata</i>	an.hort	5	0.05	Farmland	Micro
<i>Axylia putris</i>	ax.put	5	0.05	Farmland	Macro
<i>Caradrina morpheus</i>	car.morph	5	0.05	Farmland	Macro
<i>Diarsia</i> spp.	diar	5	0.05	Woody	Macro
<i>Eulithis populata</i>	eul.popul	5	0.05	Other	Macro
<i>Idaea dimidiata</i>	ida.dimidiat	5	0.05	Farmland	Macro
<i>Noctua fimbriata</i>	noc.fimb	5	0.05	Broad diet	Macro
<i>korscheltellus lupulina</i>	kor.lup	5	0.05	Farmland	Macro
<i>Cabera exanthemata</i>	cab.ex	4	0.04	Woody	Macro
<i>Cidaria fulvata</i>	cid.fulv	4	0.04	Farmland	Macro
<i>Ennomos alniaria</i>	enn.alniar	4	0.04	Woody	Macro
<i>Eudonia murana/trunciolella</i>	eud.mur/trunc	4	0.04	Farmland	Micro
<i>Gymnoscelis rufifasciata</i>	gym.ru	4	0.04	Farmland	Micro
<i>Naenia typica</i>	nae.t	4	0.04	Broad diet	Macro

<i>Pandemis heperana</i>	pand.hep	4	0.04	Woody	Micro
<i>Agonopterix anenella</i>	agon.an	3	0.03	Farmland	Micro
<i>Agrotis puta</i>	agr.put	3	0.03	Farmland	Macro
<i>Apamea crenata</i>	ap.cren	3	0.03	Farmland	Macro
<i>Apamea scolopacina</i>	ap.scol	3	0.03	Woody	Macro
<i>Argyresthia bonnetella</i>	argy.bon	3	0.03	Woody	Micro
<i>Depressaria sordidatella</i>	dep.sord	3	0.03	Farmland	Micro
<i>Elachista canapenella</i>	elac.can	3	0.03	Farmland	Micro
<i>Elophila nymphaeata</i>	elo.nym	3	0.03	Other	Micro
<i>Eucosma hohenwartiana</i>	euc.hoh	3	0.03	Farmland	Micro
<i>Eupithecia pulchellata</i>	eup.pul	3	0.03	Farmland	Macro
<i>Euxoa tritici</i>	eux.tr	3	0.03	Farmland	Macro
<i>Ourapteryx sambucaria</i>	our.sam	3	0.03	Woody	Macro
<i>Agrotis ipsilon</i>	agr.ips	2	0.02	Farmland	Macro
<i>Aphomia sociella</i>	apho.ham	2	0.02	Other	Micro
<i>Autographa pulchrina</i>	aut.pul	2	0.02	Farmland	Macro
<i>Autostichidae</i>	auto	2	0.02	Farmland	Macro
<i>Catastia marginata</i>	cat.marg	2	0.02	Farmland	Micro
<i>Cleorodes lichenaria</i>	cleo.lich	2	0.02	Other	Macro
<i>Eulithis prunata</i>	eul.pruna	2	0.02	Woody	Macro
<i>Eupithecia icterata</i>	eup.ict	2	0.02	Farmland	Macro
<i>Gillmeria pallidactyla</i>	gil.pal	2	0.02	Farmland	Micro
<i>Hadena perplexa</i>	had.perplex	2	0.02	Farmland	Macro
<i>Hylaea fasciaria</i>	hyl.fasciar	2	0.02	Woody	Macro
<i>Limnaecia phragmitella</i>	lim.phragmit	2	0.02	Other	Micro
<i>Lomaspilis marginata</i>	lom.mar	2	0.02	Woody	Macro
<i>Mesoligia furuncula</i>	mes.furu	2	0.02	Farmland	Macro
<i>Mirificarma mulinella</i>	miri.mul	2	0.02	Woody	Micro
<i>Peribatodes rhomboidaria</i>	perib.rh	2	0.02	Woody	Macro
<i>Perizoma flavofasciata</i>	periz.flavo	2	0.02	Farmland	Macro
<i>Pheosia gnoma</i>	phe.gno	2	0.02	Woody	Macro
<i>Plusia festucae</i>	plu.festuca	2	0.02	Farmland	Macro
<i>Rhopobota naevana</i>	rho.nae	2	0.02	Woody	Micro
<i>Stenoptilia pterodactyla</i>	stenop.ptero	2	0.02	Farmland	Micro
<i>Udea prunalis</i>	ud.prun	2	0.02	Broad diet	Micro
<i>Xestia stigmatica</i>	xes.stigmat	2	0.02	Woody	Macro
<i>Acompsia cinerella</i>	acompcin	1	0.01	Farmland	Micro
<i>Acronicta psi/tridens</i>	ac.psi/tri	1	0.01	Woody	Macro
<i>Agonopterix subpropinquella</i>	agon.sub	1	0.01	Farmland	Micro
<i>Agonopterix umbellana</i>	agon.umb	1	0.01	Woody	Micro
<i>Agrotis clavis</i>	agr.cla	1	0.01	Farmland	Macro
<i>Anthophila fabriciana</i>	antho.fab	1	0.01	Specialist	Micro
<i>Apamea remissa</i>	ap.rem	1	0.01	Farmland	Macro

<i>Aphelia paleana</i>	aph.pal	1	0.01	Farmland	Micro
<i>Aphelia viburnana</i>	aph.vib	1	0.01	Broad diet	Micro
<i>Apomyelois bistriatella</i>	apom.bist	1	0.01	Other	Micro
<i>Apotomis betuletana</i>	apo.bet	1	0.01	Woody	Micro
<i>Argyresthia geodartella</i>	argy.goed	1	0.01	Woody	Micro
<i>Argyresthia pygmaeella</i>	argy.pygm	1	0.01	Woody	Micro
<i>Bactrachedra praeangusta</i>	bac.pra	1	0.01	Woody	Micro
<i>Bryophila domestica</i>	bry.dom	1	0.01	Other	Macro
<i>Cabera pusaria</i>	cab.pus	1	0.01	Woody	Macro
<i>Camptogramma bilineata</i>	cmpt.bil	1	0.01	Farmland	Macro
<i>Chilodes maritima</i>	chl.mar	1	0.01	Other	Macro
<i>Chloroclystis v-ata</i>	chlor.v	1	0.01	Woody	Macro
<i>Crambus lathoniellus</i>	cram.lath	1	0.01	Farmland	Micro
<i>Cydia ulcitana</i>	cyd.uli	1	0.01	Woody	Micro
<i>Depressaria pulcherrimella</i>	dep.pul	1	0.01	Farmland	Micro
<i>Depressaria radiella</i>	dep.rad	1	0.01	Farmland	Micro
<i>Dryobotodes eremita</i>	dry.er	1	0.01	Woody	Macro
<i>Eilema depressa</i>	eil.depress	1	0.01	Other	Macro
<i>Elachista argentella</i>	elac.arg	1	0.01	Farmland	Micro
<i>Elachista maculicerusella</i>	elac.mac	1	0.01	Other	Micro
<i>Epiblema costipunctata</i>	epib.cos	1	0.01	Farmland	Micro
<i>Epinotia brunnichana</i>	epin.brun	1	0.01	Woody	Micro
<i>Eucosma campoliliana</i>	euc.cam	1	0.01	Farmland	Micro
<i>Eugnorisma depuncta</i>	eug.dep	1	0.01	Farmland	Macro
<i>Eupithecia trisignaria</i>	eup.tri	1	0.01	Farmland	Macro
<i>Euplexia lucipara</i>	eup.lucip	1	0.01	Woody	Macro
<i>Gelechia nigra</i>	gel.nig	1	0.01	Woody	Micro
<i>Herminia tarsipennalis</i>	her.tarsi	1	0.01	Other	Macro
<i>Hofmannophila pseudospretella</i>	hof.pseu	1	0.01	Specialist	Micro
<i>Lateroligia ophiogramma</i>	lat.op	1	0.01	Farmland	Macro
<i>Monochroa cystisella</i>	mon.con	1	0.01	Farmland	Micro
<i>Notocelia uddmanniana</i>	not.udd	1	0.01	Woody	Micro
<i>Orthosia cerasi</i>	ort.ceras	1	0.01	Woody	Macro
<i>Pasiphila rectangulata</i>	pas.rect	1	0.01	Woody	Macro
<i>Pennithera firmata</i>	pen.fir	1	0.01	Woody	Macro
<i>Perizoma bifaciata</i>	periz.bifac	1	0.01	Farmland	Macro
<i>Phiaris micana</i>	phi.mic	1	0.01	Broad diet	Micro
<i>Phiaris palustrana</i>	phi.pal	1	0.01	Farmland	Micro
<i>Platyptilia gonodactyla</i>	plat.gon	1	0.01	Farmland	Micro
<i>Plusia putnami</i>	plu.putnami	1	0.01	Farmland	Macro

<i>Pseudargyrotoza conwaga</i>	pseu.con	1	0.01	Woody	Micro
<i>Rhyacia simulans</i>	rhy.simula	1	0.01	Farmland	Macro
<i>Rusina ferruginea</i>	rus.ferrugi	1	0.01	Farmland	Macro
<i>Schrankia costaestrigalis</i>	sch.cost	1	0.01	Woody	Micro
<i>Scoparia pyralella</i>	scop_pyr	1	0.01	Other	Micro
<i>Spilonota laricana</i>	spil_oc/lan	1	0.01	Woody	Micro
<i>Spilonota ocellana</i>	spil_oc	1	0.01	Woody	Micro
<i>Spilosoma lubricipeda</i>	spi_lubr	1	0.01	Broad diet	Macro
<i>Tinea semifulvella</i>	tin_semi	1	0.01	Other	Micro
<i>Udea descreptalis</i>	ud_des	1	0.01	Specialist	Micro
<i>Gortyna flavago</i>	gor_flavag	1	0.01	Farmland	Macro
<i>Thyatira batis</i>	thy_batis	1	0.01	Woody	Macro
<i>Total</i>		9250			

Table S.2.7. Summary table for GLMMs comparing moth abundance, species richness and diversity in crop–crop margins and crop–grass margins on mixed farms

Response variable	Model estimate	Std error	Pr (> z)	Distribution
<i>Macro moths</i>				
Abundance	–0.19	0.16	0.2	n.binomial ^a
Species richness	–0.12	0.09	0.22	n.binomial
Diversity	–0.09	0.07	0.21	Poisson
<i>Micro moths</i>				
Abundance	0.09	0.15	0.56	n.binomial
Species richness	–0.12	0.1	0.22	n.binomial
Diversity	–0.071	0.11	0.51	Poisson
<i>Farmland macro moths</i>				
Abundance	–0.21	0.16	0.2	n.binomial
Species richness	–0.11	0.08	0.17	Poisson
Diversity	–0.1	0.08	0.25	gaussian
<i>Farmland micro moths</i>				
Abundance	0.03	0.16	0.82	n.binomial
Species richness	–0.08	0.12	0.5	poisson
Diversity	–0.08	0.12	0.5	gaussian

^a n.binomial = ‘negative binomial’

Table S.2.8.1. PERMANOVA summary table for farm-level analysis of moth community composition.

	Macro moths	Micro moths	Farmland macro moths	Farmland micro moths
Farm type	<i>ns</i> ^a	<i>ns</i>	<i>ns</i>	<i>ns</i>
Woodland edge density	<i>ns</i>	$r^2 = 0.071$ ($p = 0.037$)	<i>ns</i>	$r^2 = 0.039$ ($p = 0.039$)

Table S.2.8.2: PERMANOVA summary table for trap-level analysis of moth community composition.

	Macro moths	Micro moths	Farmland macro moths	Farmland micro moths
Margin type	<i>ns</i>	<i>ns</i>	<i>ns</i>	<i>ns</i>
Woody feature height	$r^2 = 0.030$ $p = 0.030$	$r^2 = 0.032$ $p = 0.017$	$r^2 = 0.030$ $p = 0.058$	$r^2 = 0.029$ $p = 0.032$
Crop diversity	<i>ns</i>	<i>ns</i>	<i>ns</i>	$r^2 = 0.026$ $p = 0.065$

^a'ns' = 'non-significant' ($P > 0.1$)

Chapter 3: Direct and indirect effects of mixed farming systems on nocturnal aerial invertebrates, mediated by local features and landscape attributes

Abstract

Insect populations are suffering widespread declines in different regions across the globe. Intensive farming, associated with frequent pesticide use, removal of semi-natural habitat and homogenisation of landscapes is thought to be one of the key drivers of these decline. Invertebrates provide a wide range of ecosystem services from pollination to decomposition and are also the main food source for many taxa at higher trophic levels. Thus, the loss of insects on farms will have severe repercussions for ecosystem function and could lead to cascading biodiversity decline. Mixed farming, through the integration of livestock into crop rotations, can lead to reduced synthetic inputs and a greater landscape heterogeneity. Some invertebrates also rely on dung for in their larval stage and may benefit from the presence of livestock within farmed landscapes. In this study, I assessed the direct and indirect effects (mediated by landscape attributes and local features) of mixed farming on aerial invertebrates, in comparison to arable farming where no livestock is present. I carried out light trapping on 13 mixed and 13 arable farms in East Scotland between June and August 2022. Landscape attributes and local features were more important than farm type for aerial invertebrates. Higher habitat diversity in the surrounding landscape was marginally associated with higher diversity of insect orders and Hymenoptera abundance. I found a small direct positive effect of mixed farming on Brachycera abundance (+ 5.7. %) compared to arable farming. Brachycera abundance was 20% lower on farms with sheep grazing than those with cattle only. Cattle stocking rate had a

negative effect on Trichoptera abundance and traps placed adjacent to pasture had 13.7% lower Hymenoptera abundance than those placed between crop fields. Overall, mixed farming had little benefit for nocturnal aerial invertebrates. Agricultural policies that encourage an increase in landscape scale habitat diversity and taller hedgerows could be of more benefit to insects.

3.1. Introduction

Long-term insect monitoring schemes have noted a continuous decline in the abundance, biomass and/or diversity of insects over the last few decades, both across Europe (Brooks et al., 2012b; Hallmann et al., 2017a; Møller, 2019) and North America (Forister et al., 2021). Intensive agricultural practices have been identified as one of the key drivers of these declines (Wagner, 2019). Intensive farming is characterised by the use of synthetic inputs, specialisation, and the removal of natural habitats. Synthetic fertilisers and herbicides reduce plant diversity in field margins (Schmitz et al., 2014) thus reducing diversity of food available for phytophagous insects, with pesticides known to have lethal effects on non-target invertebrates (Goebel et al., 2024; Goulson et al., 2015). Insects with aquatic larval forms can also be affected by the run-off of these agrochemicals into nearby streams and waterbodies (Gagliardi and Pettigrove, 2013; Madden et al., 1992). Specialisation of farming (usually in either livestock or arable crops) often leads to more homogenous landscapes (Garrett et al., 2020) with a low diversity of natural habitat available for invertebrates. These homogenous landscapes have been associated with simplification of insect communities (Ekroos et al., 2010; Gámez-Virués et al., 2015) and a low proportion of semi-natural area and woodland in the landscape is associated with lower aerial invertebrate abundance (Fuentes-Montemayor et al., 2011b; Garrett et al., 2022a). Areas where farmers specialise in arable crops, especially cereals, can lead to more intensive agricultural practices (such as increased

use of pesticides and fertilisers), thus the proportion cover of arable crops and cereals in the landscape can reduce insect abundance (Földesi et al., 2016; Paquette et al., 2013).

Invertebrates provide a variety of financially valuable ecosystem services including pollination, pest control and decomposition (Losey and Vaughan, 2006). Flying insects, particularly those from the order Diptera, are also an important food source for taxonomic groups at higher trophic levels such as birds and bats (Buchanan et al., 2006; Swift et al., 1985; Vesterinen et al., 2018), with some studies suggesting a parallel decline in aerial insect abundance and populations of their insectivore predators (Mammola et al., 2024; Møller, 2019). In fact, insect prey availability is positively correlated with the survival of tree swallow chicks (*Tachycineta bicolor*) and birth rate of the greater horseshoe bat (*Rhinolophus ferrumequinum*) (Garrett et al., 2022b; Mammola et al., 2024), so maintaining adequate levels of insect abundance and diversity on farms is likely to have benefits across the food web.

Prior to the industrial revolution, 'Mixed farming' was a widespread agricultural practice (Garrett et al., 2020), characterised by the integration of livestock into the crop rotation and can lead to less intensive agricultural practices than specialised farming, such as crop only or 'arable' farming (Ryschawy et al., 2012a). Indeed, livestock provide natural fertiliser for crop fields via dung as well as natural weed control (Schuster et al., 2016), with rotation of temporary grassland with crops increasing soil organic matter (Nevens and Reheul, 2002; Zani et al., 2021). Thus, mixed farming may reduce the need for synthetic inputs that are harmful to invertebrates (MacLaren et al., 2019). Greater habitat diversity on the farm provided by pasture, sheltered woodland areas for livestock and a greater diversity of crops (often grown to feed livestock) may provide more variety of food resources and habitats for insects. In addition, some insect families, particularly Scathophagidae (Diptera) and Geotrupidae, Scarabidae and Onthophagus (Coleoptera) rely on livestock dung for part of their life cycle (Schmid et al., 2024a). In addition, some

Dipterans from the Culicidea (Nematocera) family are parasitic and feed directly from livestock (Kameke et al., 2017). Therefore, areas where livestock are present can provide important feeding grounds for bats and birds by attracting insects (Ancillotto et al., 2017; Dietz et al., 2013; Evans et al., 2007). However, the species richness and abundance of parasitoids can decrease with increasing stocking rates of cattle and sheep (McMahon et al., 2012). Therefore, the effects of mixed farming on invertebrates are likely complex, as they may be both positive and/or negative as well as direct and/or indirect. Here, I take a whole-system approach using structural equation modelling to evaluate whether mixed farming has benefits over arable farming for nocturnal aerial invertebrates. Using data collected across 26 farms in North-East Scotland, I ask the following questions:

1. Is mixed farming associated with higher nocturnal aerial invertebrate abundance than arable farming, either directly or indirectly via landscape attributes or local features?
2. On mixed farms, is nocturnal insect abundance higher adjacent to pasture than in arable areas? If so, is this influenced by pasture management (e.g. livestock stocking rates)?

3.2. Method

3.2.1. Site selection

I selected 13 arable farms and 13 mixed farms across an agriculturally productive lowland area of North-East Scotland (Figure S.3.1). Farmers were recruited using social media advertising and agricultural contacts, with additional sites secured using recommendations from participating farmers. An 'arable farm' was defined as growing arable crops with no livestock present on the farm, whilst a 'mixed' farm was defined as having livestock integrated into the crop rotation, either by rotating temporary grassland with crops, and/or by grazing livestock on herbal leys or brassicas. All mixed farms were

predominantly beef cattle farms, with six out of 13 also grazing sheep. To enable the analysis of the effects of crop diversity on insects, all farms grew at least two types of crop. All farms grew at least one type of cereal (mainly wheat or barley but sometimes oats), with some farms also growing root vegetables, brassicas (mainly rapeseed) and/or fruit trees.

3.2.2. Insect sampling

For insect sampling each mixed farm was paired with a nearby arable farm (mean distance = 9.5 km, min = 3 km, max = 16 km) and farms within the same pair were surveyed for insects simultaneously using UV LED light traps, following the light trap design used in Infusino et al. (2017). Light traps are widely used to catch a range of nocturnal flying insects including Lepidoptera, Diptera, Trichoptera and many species of Coleoptera (Fuentes-Montemayor et al., 2011b; Liu et al., 2007; Waringer, 2003). Aerial invertebrate abundances are higher at field edges than in the centre of fields (Pocock and Jennings, 2008), most likely because of the shelter provided by vegetation along field margins. As such, I set up light traps adjacent to hedgerows, tree lines or woodland strips (hereafter called 'woody features') in between agricultural fields. To avoid the effects of different crop types, traps were always placed within the margins of cereal fields (either winter wheat or spring barley, as these are the two most common cereal crops in my study area). To compare insect abundance and diversity between arable and mixed farms (Q1) I placed three traps on each farm in field margins bordered by crops on both sides ('crop – crop' margins). To assess the effects of stocking rate and the importance of pasture habitat on mixed farms (Q2), I placed an additional three traps on each mixed farm in field margins adjacent to pasture ('pasture – crop' margins). Resulting in three traps on every arable farm and six traps on every mixed farm. Some traps malfunctioned (n = 6) and in some cases I were unable to place traps in pasture – crop margins due to lack of this feature on some mixed farms, where

this occurred, I only placed two pasture – crop traps on the mixed farm (n = 10). Total numbers of traps in each margin type are given in Figure 3.1

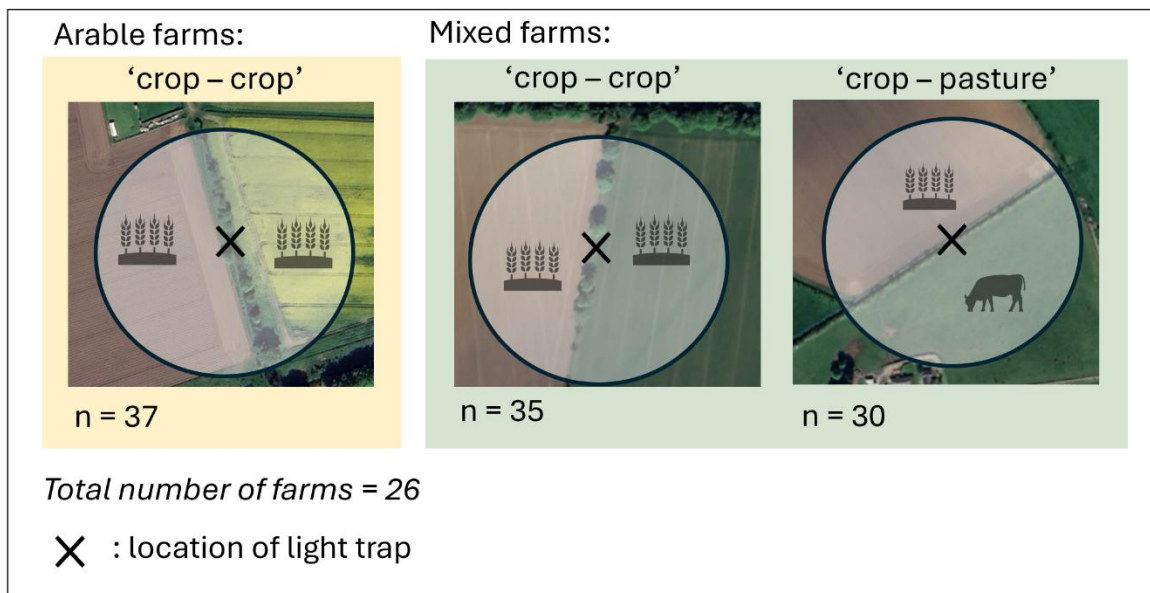


Figure 3.1. Set-up of insect traps. 'n'; is used to indicate the total number of insect traps per margin type (eg: crop – crop on arable farms, crop – crop on mixed farms and crop – pasture on mixed farms).

Insects were trapped once on each farm between mid June and mid August 2022. Light traps were set to turn on at dusk (using solar sensors) and run until dawn. Traps were collected shortly after sunrise and insects were euthanised using a cotton ball soaked in ethyl acetate. With the exception of moths (chapter 2) all insects were preserved in 70% ethanol for later identification. I identified insects to order level or sub-order for Diptera using identification keys (Unwin, 1981). For Diptera I differentiated between Nematocera whose larvae are largely aquatic and Brachycera whose larvae are often associated with animal dung and decaying matter (Farzana Khan Perveen, 2025).

Temperature at sunset was taken using a vehicle thermometer and the maximum height of woody features within 15 m either side of each trap was visually estimated (by the same surveyor each time to avoid surveyor bias). For mixed farms, information on the number of cattle, in UK livestock units (LU), was obtained from farmers, with 1 LU approximately equivalent to one beef cow and

calf (SAC Consulting, 2024a). This was then used along with the total area of grazing available, including permanent and temporary grassland, herbal leys and brassica mixes for grazing, to calculate a whole-farm stocking rate. I also recorded whether sheep were grazed on the farm.

3.2.3. Data analysis

All data analysis was carried out using R version 4.3.2.

3.2.3.1. Landscape variable selection

I re-classified the Centre of Ecology and Hydrology land cover map (Marston et al., 2022) into biotypes (table S.3.1) and created buffers of 250, 500, and 1000m around each insect trap location in QGIS version 3.28.1. (QGIS Development Team, 2021) to quantify land cover types at different scales that are relevant to flying invertebrates. The 'landscapemetrics' package in R (Hesselbarth et al., 2019) was used to extract metrics of landscape composition and configuration at each spatial scale. I based my selection of potential landscape variables on landscape attributes that are known to affect the most well-studied insect orders: proportion of arable (cereals and vegetables combined, Litovska et al., 2025), proportion of cereals (Paquette et al., 2013), proportion of woodland, woodland edge density (Garrett et al., 2022b), proportion of built-up areas (Svenningsen et al., 2024) and proportion of semi-natural, excluding woodland (Fuentes-Montemayor et al., 2011b). I also quantified Shannon's index for habitat diversity (Martin et al., 2016) which included woodland, arable, improved grassland, semi-natural, freshwater (rivers and ponds) and built-up areas. The proportion of semi-natural areas and built-up areas was very low even at the largest scale (<0.02 % and 3.5 % at the 1000 m scale respectively) so these variables were not considered for subsequent insect models. Equally, the proportion of woodland was very low at scales of

250 m ($<0.05\%$), so only scales of 500 m and 1000 m were considered for woodland metrics. Crop maps supplied by farmers, combined with ground-truthing, was used to obtain a measure of crop diversity within 250 m of each trap (larger scales were not possible for some farms as they would have encompassed land that was not part of the farm). I then classified crops into functional groups (cereals, legumes, brassicas, root vegetables, grassland, agri-environment scheme mix; Table S.3.2) similar to previous studies (Aguilera et al., 2020; Redlich et al., 2018) and obtained Shannon's diversity index for crop diversity.

Since many of the landscape variables considered correlated (Table S.3.2) and to avoid over-fitting models, I used r^2 values to select variables that were most likely to explain the greatest amount of variation in insect abundances. I modelled the response of each insect group (Nematocera, Brachycera, Hymenoptera, Hemiptera, Coleoptera, Trichoptera and Shannon's diversity of insect orders/sub-orders) against each landscape variable and at each spatial scale separately using generalised linear models (GLMs). All count data was modelled using a Poisson distribution and the lme4 package (Douglas Bates et al., 2015), unless over dispersion was detected, in which case I applied a negative binomial distribution using the MASS package (Venables and Ripely, 2002). Insect diversity index was modelled using a gaussian distribution and the lme4 package. An r^2 value was obtained for each model (Figure. S.2) using Nagelkerke's pseudo r^2 for count data (Nagelkerke, 1991). One metric of landscape composition and one metric of landscape configuration was selected for final models, as well as the most relevant scale for each metric, based on r^2 values. Proximity of each trap to the nearest freshwater body (rivers, ponds and lakes) and buildings was manually measured in QGIS using OS Mastermap (Ordnance Survey GB, 2023).

3.2.3.2. Assessing direct and indirect effects of mixed farming

To assess the direct and indirect effects of mixed farming on aerial invertebrates (Q1), I used structural equation modelling (SEM). SEM is a multivariate technique that allows the testing of hypothesized causal relationships between multiple response variables in a system, allowing for the detection of direct effects and indirect effects mediated by other variables. I built SEMs using the *piecewiseSEM* package in R, as this allows for non-normal distributions and random effects.

Using data from crop-crop field margins, separate SEMs were built for Nematocera, Brachycera, Coleoptera, Hymenoptera, Hemiptera, Trichoptera and insect order diversity index. For each insect group I included 'farm type' (either arable or mixed) as a fixed effect as well as the two measures of landscape composition with the highest r^2 value (section 2.3.1). In some cases, the two landscape measures with the highest r^2 were closely correlated (Pearson > 0.6). In this case, only the measure with the highest r^2 was included. Crop diversity within 250 m of the trap was included as a fixed effect for all insect groups that are phytophagous in either adult or larval form (Hemiptera and Coleoptera) as well as for insect diversity index. Sheltered areas are important for invertebrates in open landscapes (Merckx et al., 2010), thus I included height of the woody feature adjacent to traps. In addition, for Nematocera and Trichoptera I included 'proximity to water' as these insect orders have aquatic larval stages. Brachycera and their predators have been associated with farmland buildings (Dietz et al., 2013; Nosal et al., 2019, chapter 4) so I included 'proximity to farm buildings' for the Brachycera sub-order. Temperature can drive insect abundances and trigger emergences, so this was included in all SEMs. In some cases, insect abundances showed a non-linear relationship with temperature, in which case it was included as a quadratic effect. Finally, all SEM models also included the random effect of 'Farm' to account for survey design (i.e. multiple traps per farm) and avoid pseudo-replication. When random effect variance was negligible (< 0.0001) this was removed from the model. All count data was modelled using a Poisson

distribution unless overdispersion was detected, in which case I used a negative binomial distribution. Coleoptera abundance showed underdispersion, so this was modelled as a binomial response. Insect diversity index was modelled using a Gaussian distribution. All continuous variables were scaled to 1 standard deviation (SD) and centred around the mean. Once SEMs were built I tested for missing pathways using the test of directed separation (Shipley, 2000) and Fisher's C statistic (which tests whether the data fit the hypothesized SEM). If missing pathways were significant ($p < 0.05$) I included these as correlated errors only if they improved model fit (Fisher's C statistic $p > 0.05$).

3.2.3.3. Assessing the importance livestock stocking rate and pasture presence

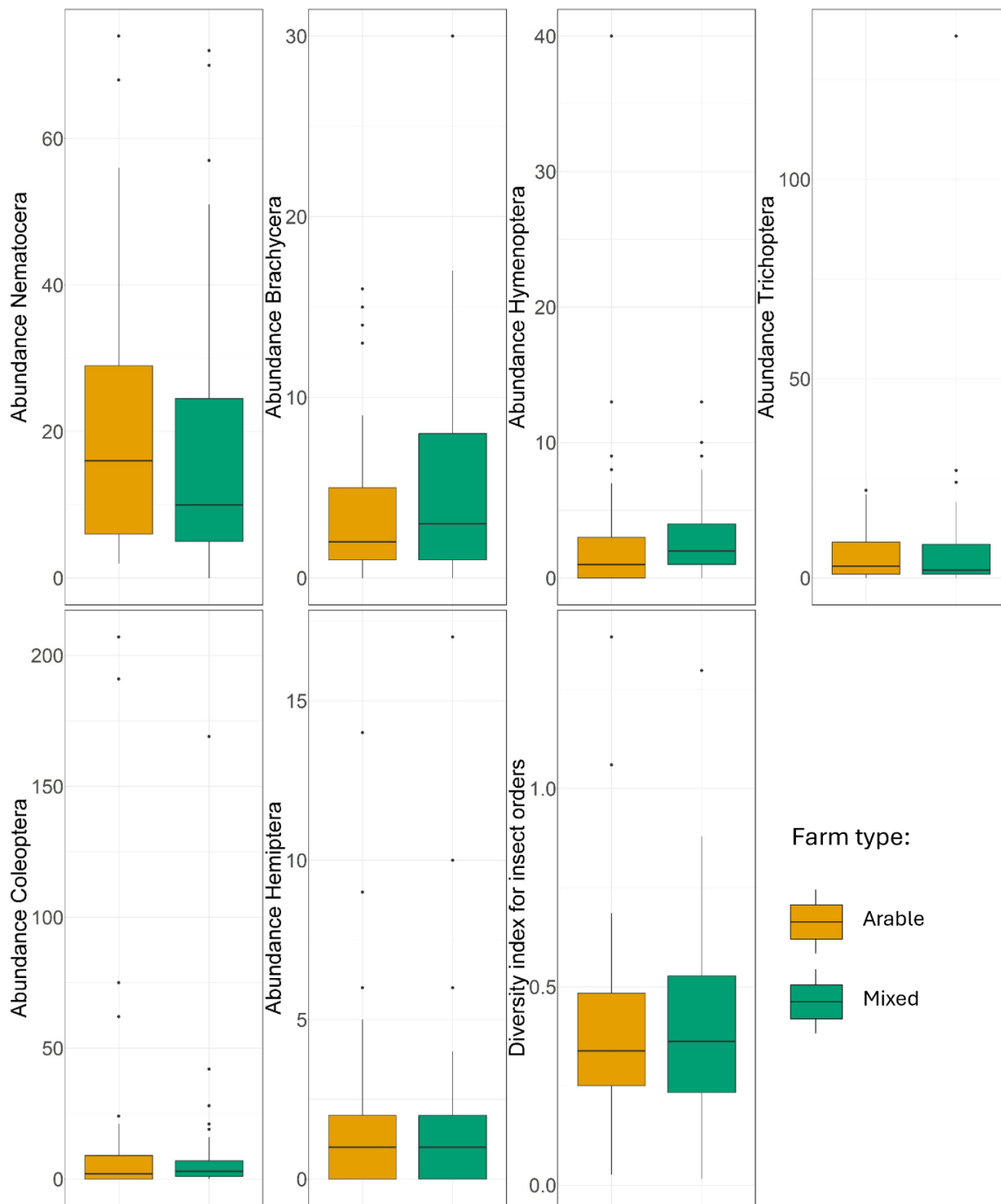
To assess the effects of whole-farm stocking rate and the value of pasture for aerial insects (Q2), I used data from traps placed on mixed farms only ($n = 65$). I built GLMMs separately for each insect group (Nematocera, Brachycera, Coleoptera, Hymenoptera, Hemiptera, Trichoptera and insect order diversity). GLMMs were built with the glmmTMB package (Brooks et al., 2017). 'Farm' was included in all models as a random effect to account for multiple samples per farm. I included 'margin type' as a fixed effect to compare insect abundance next to pasture (crop-pasture margins) with abundances between two crop fields (crop – crop margins). Woody feature height adjacent to traps was also included as this was highly variable within each farm. I did not include temperature since this was the same for all traps within the same farm, so variation due to temperature was accounted for in the random effect. Whole-farm cattle stocking rate was incorporated as a fixed effect (in LUs per hectare of grazing available), and the presence/absence of sheep grazing as a categorical effect. Continuous variables were scaled (to 1 SD) and centred around the mean. All count data was modelled with a Poisson distribution,

unless overdispersion was detected in which case I used a negative binomial distribution. Insect diversity was log transformed to achieve normality and modelled using a Gaussian distribution.

3.3. Results

3.3.1. Overview

I collected a total of 16,732 individual insects across 112 light traps. Trap catch was primarily composed of Lepidoptera (57%, results published in Kennedy et al., (2026)) followed by Nematocera (15%), Coleoptera (12%), Trichoptera (5%) and Brachycera (3%). Remaining insect orders made up less than 8% of the total catch. Hemiptera were found in over 50% of all traps, though usually in low numbers (mean = 1.7, SD = 2.8). Ephemeroptera, Chrysopidae and Neuroptera were found in a small number of traps ($n \leq 8$), but not sufficient for statistical analysis. Median abundance of each insect order/sub-order was similar between mixed and arable farms (Figure 3.2).



arable farms at 250 and 500 m but not at 1000 m (Figure. 3.3b, c, e). The proportion of woodland and woodland edge density at the 1000 m scale were marginally higher on mixed farms than on arable farms ($p = 0.04$, $p = 0.07$ respectively, Figure 3.3d), whilst the proportion of cereals was significantly higher on arable farms than on mixed farms at the 1000m scale (Figure 3.3b) and marginally ($0.1 > p > 0.05$) at the 500 m scale (Figure 3.3g). The height of woody features was significantly lower on mixed farms (mean = 11 m) than on arable farms (mean = 16 m).

Farm type had both direct and indirect effects (mediated by local features and/ or landscape attributes) on some insect orders. Mixed farming had a significant positive direct effect on Brachycera, increasing abundance by an average of 5.7% ($\pm 2.8\%$). Higher abundance of Brachycera was associated with taller woody features, with a small increase in Brachycera abundance of 1.5% ($\pm 0.4\%$) associated with every 2 m increase in woody feature height. However, woody features were marginally lower on mixed farms than on arable farms, leading to an overall negative effect of mixed farming on Brachycera (Figure 3.3b).

Distance from water was the most important predictor of Trichoptera abundance, which was higher closer to freshwater bodies, decreasing by 10% ($\pm 1\%$) with every 200 m distance from water. Woody feature height had a negative effect on Trichoptera, though the effect was only marginal and was very small, with abundance reducing by just 0.8% ($\pm 0.26\%$) with every 2 m increase in woody feature height. Since woody features tended to be marginally lower on mixed farms, this resulted in a marginal indirect positive effect of mixed farming on Trichoptera abundance.

Higher habitat diversity within 1000m of the trap was significantly associated with higher Hymenoptera abundance. Habitat diversity within 250 m also had a marginal positive effect on the diversity of insect orders. Given that habitat diversity at this smaller scale was significantly higher on mixed

farms, mixed farming had an overall positive indirect effect on insect diversity (+ 26%).

There were no effects of landscape composition or configuration on Nematocera, Brachycera, Coleoptera, Hemiptera or Trichoptera. Temperature was the only predictor of Nematocera, Coleoptera and Hemiptera abundance and was also an important predictor of Brachycera abundance and the diversity of insect orders/ sub-orders.

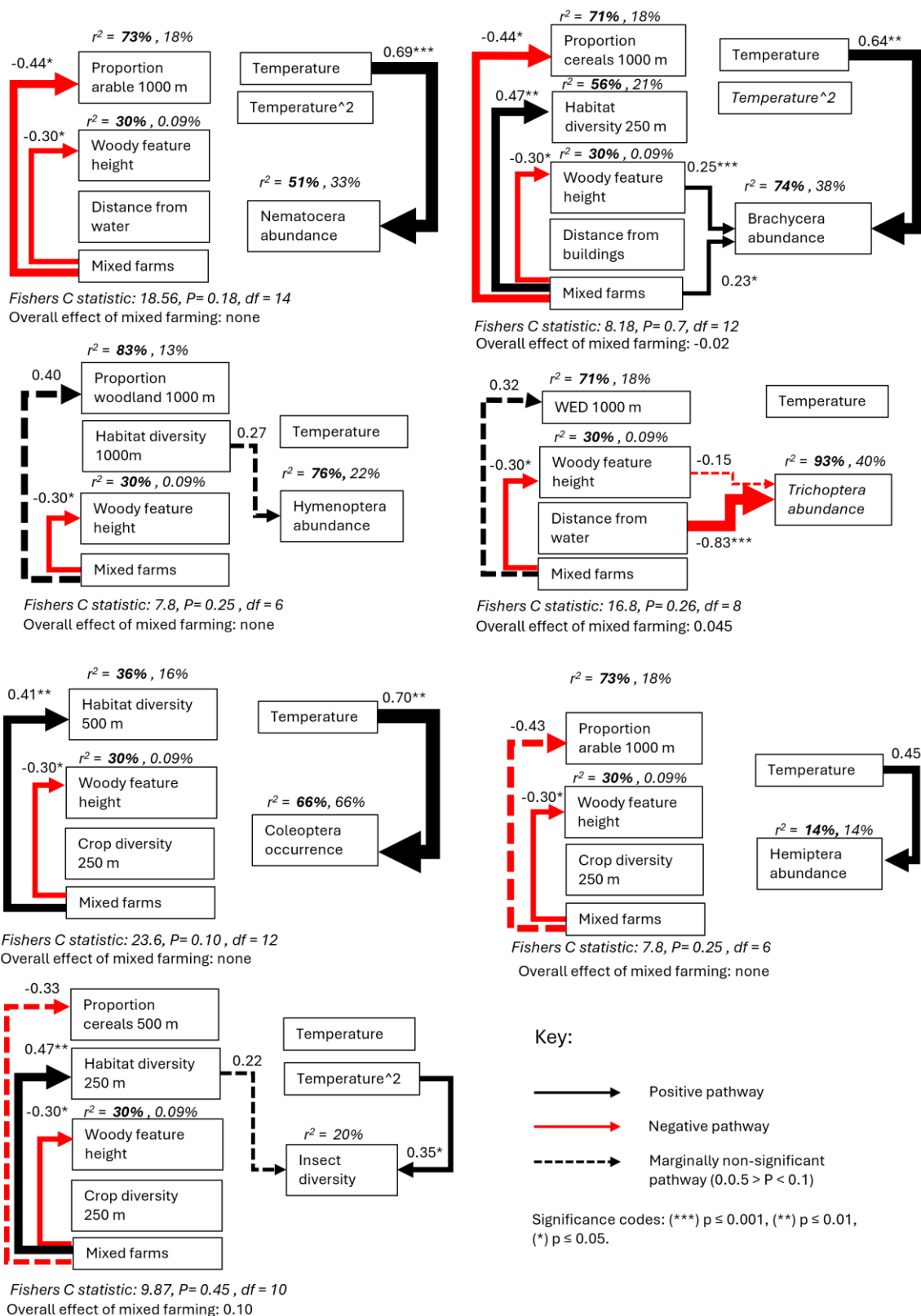


Figure 3.3: SEM path diagrams showing significant and marginally significant ($P \geq 0.05$) pathways. Where a pathway is significant an r^2 value is given above the response variable (in bold italic for conditional r^2 and italic for marginal r^2). WED = woodland edge density.

3.2.3. Effects of pasture and livestock stocking rate on invertebrates

The abundance of Brachycera was 20% ($\pm 9.6\%$) lower on mixed farms where sheep were grazed than on farms with no sheep grazing (Table 3.1, Figure S.3.4.). Hymenoptera abundance was 13.7% ($\pm 6.8\%$) lower in traps adjacent to pasture than in crop-crop margins (Figure 3.4). Higher cattle stocking rates were significantly associated with lower Trichoptera abundance, with abundance decreasing by 5.1 % ($\pm 2.6\%$) with every 1 LU Ha⁻¹ (Figure S.3.4.), the equivalent of one additional cow and calf per hectare. The amount of variation in insect abundance or diversity explained by fixed effects was relatively low (7 – 33 %), with a large amount of the variation in insect abundance being explained by the random effect of farm (Table 3.1).

Table 3.1. GLMM output summary table for the effects of pasture and livestock stocking rate on aerial invertebrates

Response	Estimate	SE	P value	R ² value (conditional, marginal)
<i>Coleoptera (negative binomial)</i>				
Field type (crop–pasture)	0.42	0.43	0.33	74%, 11%
Tree height	0.13	0.26	0.64	
Stocking rate cattle	−0.43	0.47	0.37	
Sheep presence	−1.09	0.97	0.26	
<i>Hemiptera (negative binomial)</i>				
Field type (crop–pasture)	−0.37	0.39	0.35	69%, 33%
Tree height	−0.07	0.19	0.73	
Stocking rate cattle	−0.12	0.16	0.72	
Sheep presence	−0.72	0.39	0.19	
<i>Hymenoptera (Poisson)</i>				
Field type (crop–pasture)	−0.34	0.17	0.05 ^{*a}	68%, 16%
Tree height	−0.07	0.10	0.50	
Stocking rate cattle	−0.12	0.25	0.63	
Sheep presence	−0.72	0.51	0.16	
<i>Nematocera (negative binomial)</i>				
Field type (crop–pasture)	0.15	0.17	0.38	71%, 16%
Tree height	0.04	0.09	0.67	
Stocking rate cattle	0.12	0.18	0.49	
Sheep presence	−0.45	0.38	0.24	
<i>Brachycera (negative binomial)</i>				
Field type (crop–pasture)	−0.31	0.24	0.19	59%, 28%
Tree height	0.23	0.14	0.09.	
Stocking rate cattle	−0.12	0.21	0.56	
Sheep presence	−0.94	0.45	0.04 [*]	
<i>Trichoptera (negative binomial)</i>				
Field type (crop–pasture)	−0.12	0.10	0.22	91%, 29%
Tree height	0.14	0.06	0.02 [*]	
Stocking rate cattle	−0.60	0.28	0.03 [*]	
Sheep presence	−0.45	0.56	0.43	
<i>Diversity (gaussian)</i>				
				18%, 7%
Field type crop–pasture	0.17	0.22	0.45	
Tree height	0.11	0.12	0.36	
Stocking rate	0.08	0.15	0.59	
Sheep presence	−0.35	0.29	0.23	

^asignificance codes: '*' $p \leq 0.05$, '**' $p \leq 0.01$, '***' $p \leq 0.001$. Significant results

($p < 0.05$) are given in bold

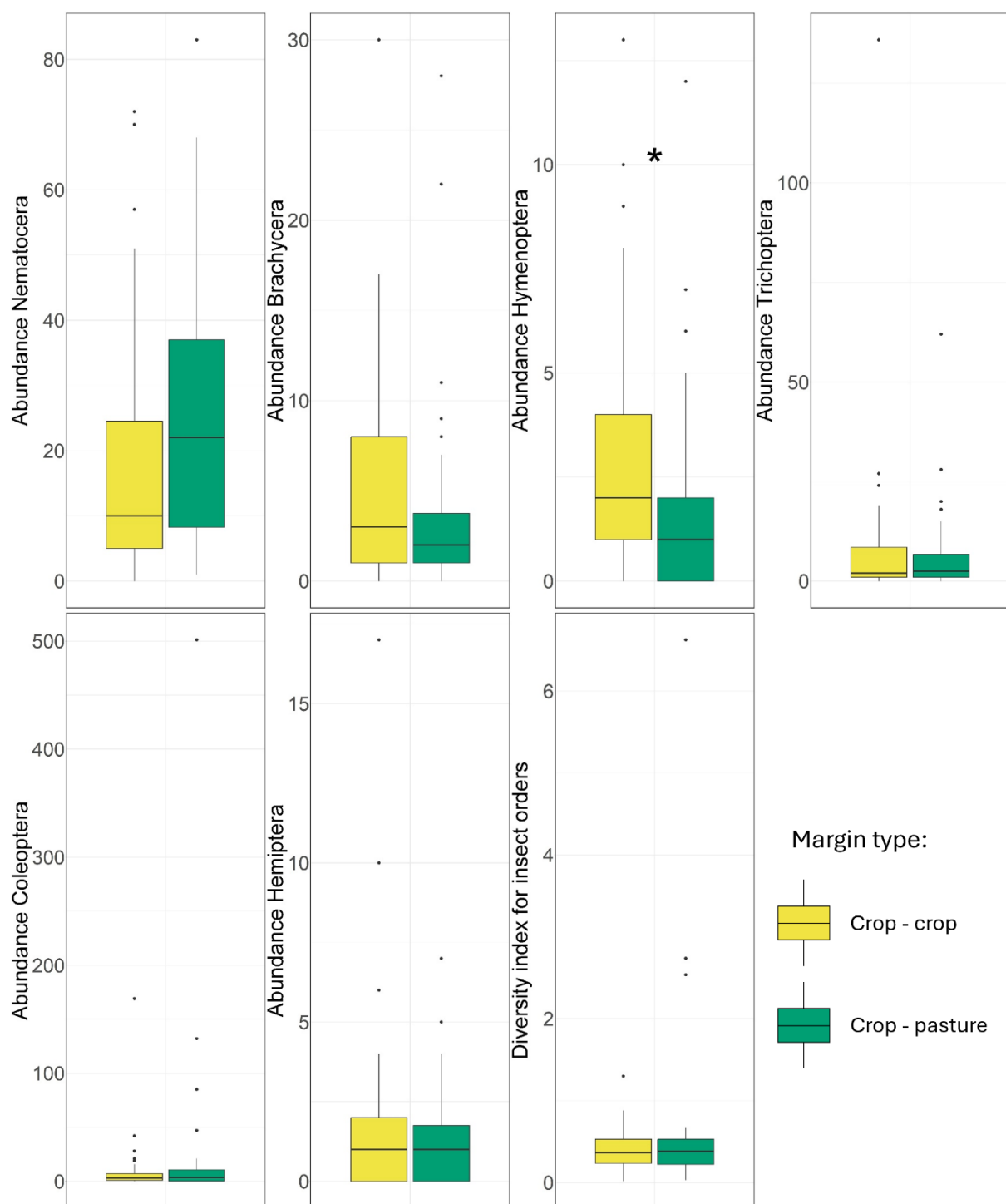


Figure 3.4: Boxplots showing abundance and diversity of aerial insects in traps placed in crop-crop margins and traps placed in crop-pasture margins. significance codes: '*' $p \leq 0.05$, '**' $p \leq 0.01$, '***' $p \leq 0.001$

3.4. Discussion

Studies on the effects of agricultural landscapes on invertebrates have been identified as a key research priority (Luke et al., 2023). I assessed the direct and indirect effects (mediated by landscape attributes and local features) of mixed farming on the abundance and diversity of aerial invertebrates. Mixed farming had no direct or indirect effect on the abundance of most invertebrate orders. The most notable effect of mixed farming was an increase in the diversity of insect orders mediated by higher habitat diversity on mixed farms. I also found a small direct positive effect of mixed farming on Brachycera abundance. However, mixed farms with higher cattle stocking rates reduced Trichoptera abundance and the presence of sheep grazing reduced Brachycera abundance.

3.4.1. Direct effects of farm type

The only insect order to be directly affected by farming type was Brachycera. Mixed farming had a direct positive effect on Brachycera abundance compared with arable farming, though the difference was only small. The high diversity of life strategies within this group make it difficult to identify potential drivers behind higher abundances on mixed farms, though this positive effect could be due to livestock dung providing a resource for the larval stages of some Brachycera species (Gröebler et al., 2010; Orłowski and Karg, 2013). The fact that the difference in Brachycera abundance between arable and mixed farms is not larger could be due to the use of anthelmintic wormers on mixed farms that have a negative effect on Brachycera (Jochmann et al., 2016).

3.4.2. Indirect effects of mixed farming mediated by landscape attributes

Habitat diversity was higher on mixed farms than on arable farms at scales of 250 m and 500 m, which could be due to a combination of greater proportion of woodland and grassland which is absent or scarce on arable farms. There were indirect benefits of mixed farming for insect diversity via increased habitat diversity at the 250 m scale. Whilst I only identified insects to order level (or sub-order for Diptera) I was still able to detect effects of the surrounding landscape on insect diversity. Thus, increasing habitat diversity on farms is likely to benefit a range of insect groups. However, mixed farming was not associated with higher habitat diversity at larger scales that were relevant for Hymenoptera, which benefitted from greater habitat diversity at the 1000 m scale, similarly to (Liu et al., 2016) and (Zhao et al., 2014). Nocturnal Hymenoptera caught in this study were largely parasitic wasps and are capable of reducing crop damage from herbivorous insects (Zhang et al., 2024). Thus, higher habitat diversity at the landscape scale, regardless of farm type is likely to increase abundance of parasitic wasps with potential benefits for natural insect pest regulation.

I did not find any effects of crop diversity on any of the insect orders where it was included in SEMs. In addition, r^2 values for the effect of crop diversity on each insect group were very low when assessed on its own (Figure. S.3.2.). The lack of effect of crop diversity on insect abundances could be due to very low amounts of semi-natural area in the landscapes surrounding study sites (> 0.02 % at the 1000 m scale). In fact Aguilera et al. (2020) have found that increasing crop diversity is only effective if enough semi-natural habitat is present (30 %).

Neither Hemiptera nor Coleoptera responded to landscape or local variables included in models (other than temperature). This could be because light trapping only targeted flying species from these groups. However, many species of Coleoptera and Hemiptera are ground-dwelling or stay on host plants, only flying sporadically. Light trapping has been successfully used to survey Nematocera (Fuentes-Montemayor et al., 2011b). However, I found no

effect of any landscape attributes or local features on Nematocera. This may be due to this aggregate group being composed of many families and species with different habitat requirements.

3.4.3. Importance of local woody features

Woody feature height was a significant predictor of Brachycera abundance, which was positively associated with taller woody features, though the effect was small. This is similar to findings in Froidevaux et al. (2019) and taller woody features may be providing sheltered areas for aerial invertebrates in what are otherwise very open landscapes (Merckx et al., 2010). However, hedgerows and tree lines were significantly lower on mixed than on arable farms, possibly as a result of browsing from livestock or a consequence of trimming practices to produce denser, livestock-proof hedges. Whilst current government policies in Scotland encourage trimming hedges in rotation across the farm, to ensure a continuous provision of nectar sources (Scottish Government, 2023), the minimum hedgerow height for obtaining government financial reward is currently set to just 1.5 m. Thus, there is currently no requirement or encouragement for farmers to grow taller hedgerows which could be more beneficial for invertebrates (maximum Brachycera abundance on farms was recorded adjacent to 25 m high woody features).

3.4.4. Livestock management on mixed farms

I found negative effects of cattle stocking rate and sheep grazing on some insect groups. Trichoptera abundance declined with increases in cattle stocking rate and Brachycera abundance was significantly lower on mixed farms that grazed sheep. Larval stages of Trichoptera are aquatic and sensitive to pollution in their freshwater environment (Erdoğan et al., 2025). It is possible

that run-off from mixed farms with higher stocking rates into local streams could be increasing the amount of nitrogen (from dung) and/or levels of anthelmintic wormers (Hooda et al., 2000) in water that is used by Trichoptera in their larval stage. Whilst there is limited research on the effects of anthelmintics on non-target invertebrates, lethal and sub-lethal effects have been found on dung beetles and Brachyceran flies (Jochmann et al., 2016; Manning et al., 2018) so these toxic effects may extend to other insect orders such as Trichoptera. A catchment-scale approach could be more appropriate in understanding the effects of stocking rate on Trichoptera.

Finally, I found lower Hymenoptera abundance in crop-pasture than in crop-crop traps. Parasitic wasp abundance can be driven by the abundance of prey (usually Lepidoptera or Hemiptera). In fact, in a parallel study (chapter 2, (Kennedy et al., 2026)) Lepidoptera abundance was also lower in traps adjacent to pasture. The lack of any differences in Diptera abundance between crop-crop and crop-pasture field margins is surprising given that other studies have found that Diptera abundance was three times higher over grazed pasture than over cereal, even where livestock were not present in fields (Evans et al., 2007). In my study farms it could be that pasture may not be providing higher quality habitat in comparison to crop fields due to livestock management practices, particularly since in Evans et al., (2007) only a small proportion of cattle were treated with anthelmintic wormers.

3.4.5. Management recommendations

I assessed the direct and indirect effects of mixed farming in comparison to arable farming on the abundance and diversity of flying invertebrates, as well as the effects of livestock stocking rates and the presence of sheep. Whilst I detected some small benefits of mixed farming for Brachycera and Hymenoptera, it is unlikely that mixed farming alone can increase aerial insect abundance and diversity on farms enough to benefit

insectivore predators or contribute to increasing biodiversity on the farm. In my study, landscape and local features were more important than farm type. Habitat diversity increased both insect diversity and Hymenoptera abundance, at smaller (250 m) and larger scales (1000 m) respectively, highlighting that increasing habitat diversity at the landscape-scale can benefit a range of insect orders. Sheep grazing substantially reduced Brachycera abundance in comparison to mixed farms with cattle only and higher stocking rates were associated with lower Trichoptera abundance. Further research into the combined effects of mixed farming with other environmentally-friendly farming practices, such as reduced synthetic inputs, reduced stocking rates and/or insect-friendly livestock management is needed to understand if mixed farming can be an approach to increasing biodiversity on farms.

Acknowledgements

I would like to thank all landowners for granting access to their land, as well as Charlotte Wood for assisting with fieldwork and identification of insects in the lab. The data collection for this chapter was fully funded by SRUC

Supplementary material chapter 3

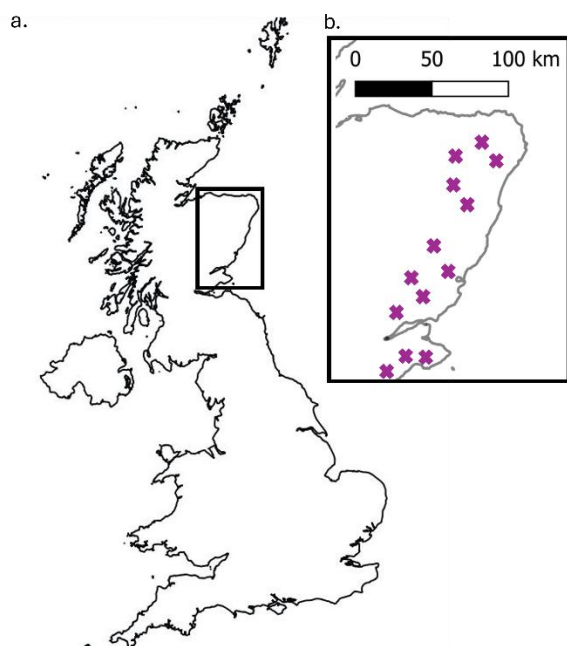


Fig S.3.1. Map showing a. location of study area and b. approximate locations of study sites. Pairs of sites are designated by a purple 'x', with each farm within a pair no more than 16km apart.

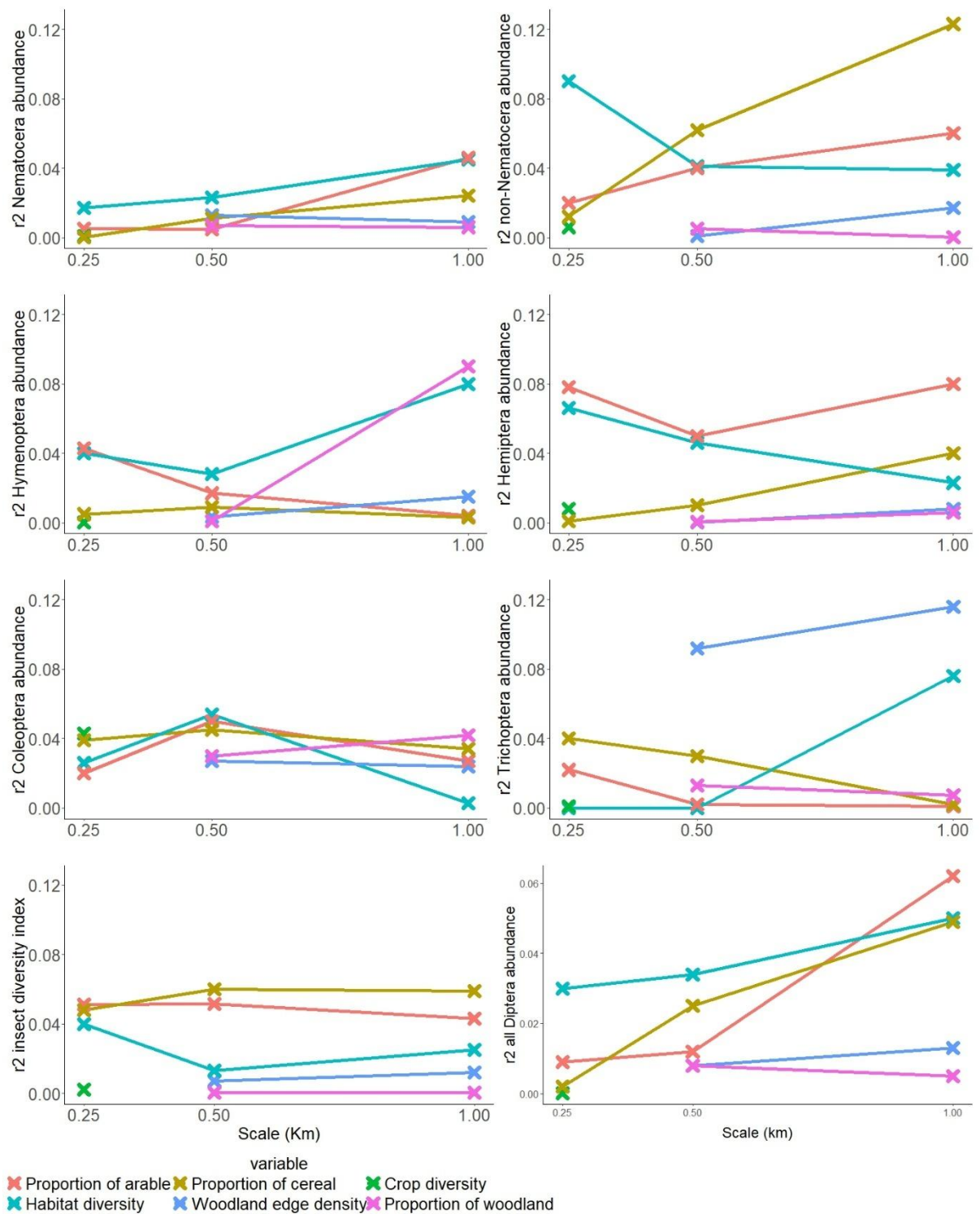


Figure S.3.2. R^2 values obtained for different landscapes metrics at different scales

Table S.3.1. Reclassification of habitat types from land cover maps into biotypes

UKCEH Land Cover Class	Assigned category
Deciduous woodland	Woodland
Coniferous woodland	Woodland
Arable	Arable
Improved grassland	Improved grassland
Neutral grassland	Semi-natural
Calcareous grassland	Semi-natural
Acid grassland	Semi-natural
Fen	Semi-natural
Heather	Semi-natural
Heather grassland	Semi-natural
Bog	Semi-natural
Inland rock	Semi-natural
Saltwater	Coastal
Freshwater	Freshwater
Supralittoral rock	Coastal
Supralittoral sediment	Coastal
Littoral rock	Coastal
Littoral sediment	Coastal
Saltmarsh	Coastal
Urban	Built
Suburban	Built

Table S.3.2. Grouping of crops into functional groups

Crop functional group	Crops included
Cereals	Barley, wheat, oats.
Legumes	Peas, beans.
Brassicas	Oilseed rape, cauliflower, Brussel sprouts, broccoli.
Root vegetables	Potatoes, carrots, sudes, turnips.
Grassland	Permanent pasture, temporary pasture and herbals leys (including clover – legume mixes).
Agri-environment scheme mix (AES)	Any seed mix sown as a part of agri-environment schemes such as bird mix, pollinator mix, wildflower mix etc.

Tables S.3.3: Correlation matrix of landscape variables

	Dist nearest building	Tree height	Temperature	Distance from water	WED 500m ^a	WED 1000m	Habitat diversity 250m	Habitat diversity 1000m	Habitat diversity 500m	% arable 250m	% arable 500m	% arable 1000m	Crop div 250m	% cereals 250m	% cereals 500m	% cereals 1000m	% woodland 500m	% woodland 1000m
Distance from buildings	1.00	0.08	-0.01	-0.21	0.35	0.02	-0.14	-0.24	-0.08	0.07	0.07	0.14	-0.14	-0.18	-0.13	-0.04	0.25	0.01
Woody feature height	0.08	1.00	-0.13	-0.17	0.30	0.06	-0.02	-0.23	0.00	-0.17	0.00	0.06	-0.13	-0.09	-0.02	0.03	0.12	-0.02
Temperature	-0.01	-0.13	1.00	-0.20	-0.07	0.14	0.12	0.18	0.23	-0.16	-0.20	-0.30	-0.03	-0.05	-0.11	-0.28	-0.07	-0.15
Distance from water	-0.21	-0.17	-0.20	1.00	-0.20	-0.08	-0.11	0.05	-0.17	0.11	0.05	-0.01	0.07	0.01	0.05	-0.02	-0.13	0.11
WED 500m	0.35	0.30	-0.07	-0.20	1.00	0.45	0.38	-0.04	0.52	-0.52	-0.54	-0.39	-0.11	-0.19	-0.31	-0.39	0.75	0.48
WED 1000m	0.02	0.06	0.14	-0.08	0.45	1.00	0.66	0.36	0.49	-0.38	-0.39	-0.64	0.10	0.11	-0.02	-0.44	0.22	0.42
Habitat diversity 250m	-0.14	-0.02	0.12	-0.11	0.38	0.66	1.00	0.59	0.81	-0.55	-0.69	-0.82	0.01	-0.06	-0.28	-0.53	0.36	0.52
Habitat diversity 1000m	-0.24	-0.23	0.18	0.05	-0.04	0.36	0.59	1.00	0.44	-0.23	-0.44	-0.59	0.09	0.21	0.00	-0.21	-0.03	0.23
Habitat diversity 500m	-0.08	0.00	0.23	-0.17	0.52	0.49	0.81	0.44	1.00	-0.63	-0.83	-0.76	-0.12	-0.03	-0.36	-0.52	0.47	0.43
% arable 250m	0.07	-0.17	-0.16	0.11	-0.52	-0.38	-0.55	-0.23	-0.63	1.00	0.80	0.62	0.05	0.04	0.16	0.30	-0.42	-0.31
% arable 500m	0.07	0.00	-0.20	0.05	-0.54	-0.39	-0.69	-0.44	-0.83	0.80	1.00	0.82	0.03	-0.02	0.34	0.49	-0.46	-0.38
% arable 1000m	0.14	0.06	-0.30	-0.01	-0.39	-0.64	-0.82	-0.59	-0.76	0.62	0.82	1.00	-0.09	-0.06	0.22	0.64	-0.34	-0.50

Crop diversity 250m	-0.14	-0.13	-0.03	0.07	-0.11	0.10	0.01	0.09	-0.12	0.05	0.03	-0.09	1.00	-0.37	-0.27	-0.21	-0.17	-0.09
% cereals 250m	-0.18	-0.09	-0.05	0.01	-0.19	0.11	-0.06	0.21	-0.03	0.04	-0.02	-0.06	-0.37	1.00	0.67	0.27	-0.16	-0.02
% cereals 500m	-0.13	-0.02	-0.11	0.05	-0.31	-0.02	-0.28	0.00	-0.36	0.16	0.34	0.22	-0.27	0.67	1.00	0.70	-0.22	-0.07
% cereals 1000m	-0.04	0.03	-0.28	-0.02	-0.39	-0.44	-0.53	-0.21	-0.52	0.30	0.49	0.64	-0.21	0.27	0.70	1.00	-0.26	-0.35
% woodland 500m	0.25	0.12	-0.07	-0.13	0.75	0.22	0.36	-0.03	0.47	-0.42	-0.46	-0.34	-0.17	-0.16	-0.22	-0.26	1.00	0.69
% woodland 1000m	0.01	-0.02	-0.15	0.11	0.48	0.42	0.52	0.23	0.43	-0.31	-0.38	-0.50	-0.09	-0.02	-0.07	-0.35	0.69	1.00

^aWED = woodland edge density

Table S.3.4: Full SEM results for nocturnal aerial invertebrates

Response	Predictor	Estimate	Std error	DF	P value	Std estimate
Brachycera abundance						
Brachycera abundance	Farm type (mixed)	0.26	0.13	72.00	0.05	0.24 *
Brachycera abundance	Tree height	0.28	0.08	72.00	<0.0001	0.25 ***
Brachycera abundance	Distance from nearest building	-0.07	0.08	72.00	0.41	-0.06
Brachycera abundance	Temperature	0.70	0.23	72.00	0.00	0.64 **
Brachycera abundance	Temperature ²	-0.18	0.18	72.00	0.30	-0.23
Brachycera abundance	Proportion cereals 1000m	-0.09	0.15	72.00	0.56	-0.08
Brachycera abundance	Habitat diversity 250m	0.06	0.11	72.00	0.56	0.06
Tree height	Farm type (mixed)	-0.30	0.14	23.20	0.04	-0.30 *
Proportion cereals 1000m	Farm type (mixed)	-0.44	0.16	23.87	0.01	-0.44 *
Habitat diversity 250m	Farm type (mixed)	0.46	0.15	23.67	0.00	0.47 **
~~Habitat diversity 250m	~~Proportion cereals 1000m	-0.50	-	72.00	0.00	-0.50 ***
~~Temperature ²	~~Proportion cereals 1000m	-0.14	-	72.00	0.12	-0.14
Nematocera abundance						
Nematocera abundance	Arable 1000m	0.00	0.14	72.00	0.99	0.00
Nematocera abundance	Tree height	-0.06	0.11	72.00	0.60	-0.06

Nematocera abundance	Distance from water	-0.12	0.10	72.00	0.22	-0.13	
Nematocera abundance	Temperature	0.69	0.16	72.00	0.00	0.71	***
Nematocera abundance	Temperature ²	-0.18	0.11	72.00	0.11	-0.25	
Nematocera abundance	Farm type (mixed)	-0.05	0.13	72.00	0.72	-0.05	
Tree height	Farm type (mixed)	-0.30	0.14	23.20	0.04	-0.30	*
Arable 1000m	Farm type (mixed)	-0.43	0.16	23.90	0.01	-0.44	*

Coleoptera occurrence

Coleoptera abundance	Farm type (mixed)	0.64	0.40	72.00	0.11	0.21	
Coleoptera abundance	Habitat diversity 500m	0.66	0.41	72.00	0.11	0.21	
Coleoptera abundance	Tree height	0.47	0.38	72.00	0.21	0.15	
Coleoptera abundance	Temperature	2.17	0.74	72.00	0.00	0.70	**
Coleoptera abundance	Crop div 250m	-0.19	0.36	72.00	0.60	-0.06	
Tree height	Farm type (mixed)	-0.30	0.14	23.20	0.04	-0.30	*
Crop div 250m	Farm type (mixed)	-0.01	0.12	22.35	0.92	-0.01	
Habitat diversity 500m	Farm type (mixed)	0.40	0.13	23.21	0.01	0.41	**

Hemiptera abundance

Hemiptera abundance	Farm type (mixed)	0.16	0.20	72.00	0.44	0.10	
Hemiptera abundance	Arable 1000m	-0.27	0.21	72.00	0.19	-0.17	
Hemiptera abundance	Tree height	0.20	0.19	72.00	0.30	0.12	
Hemiptera abundance	Temperature	0.71	0.23	72.00	0.00	0.45	**
Hemiptera abundance	Temperature ²	-0.17	0.16	72.00	0.29	-0.14	

Hemiptera abundance	Crop div 250m	0.26	0.18	72.00	0.16	0.16	
Tree height	Farm type (mixed)	-0.30	0.14	23.20	0.04	-0.30	*
Arable 1000m	Farm type (mixed)	-0.43	0.16	23.90	0.01	-0.44	*
Crop div 250m	Farm type (mixed)	-0.01	0.12	22.35	0.92	-0.01	

Hymenoptera abundance

Hymenoptera abundance	Farm type (mixed)	0.09	0.18	72.00	0.62	0.06	
Hymenoptera abundance	Proportion wood 1000m	-0.20	0.14	72.00	0.17	-0.14	
Hymenoptera abundance	Habitat diversity 1000m	0.39	0.20	72.00	0.05	0.28	
Hymenoptera abundance	Tree height	0.07	0.10	72.00	0.50	0.05	
Hymenoptera abundance	Temperature	0.41	0.26	72.00	0.11	0.29	
Tree height	Farm type (mixed)	-0.30	0.14	23.20	0.04	-0.30	*
Proportion wood 1000m	Farm type (mixed)	0.40	0.19	23.97	0.05	0.40	
Habitat diversity 1000m	Farm type (mixed)	0.17	0.18	23.99	0.37	0.17	

Trichoptera abundance

Trichoptera abundance	Farm type (mixed)	0.07	0.20	72.00	0.71	0.05	
Trichoptera abundance	Tree height	-0.16	0.09	72.00	0.07	-0.12	
Trichoptera abundance	Temperature	0.24	0.26	72.00	0.36	0.18	
Trichoptera abundance	Distance from water	-0.84	0.07	72.00	0.00	-0.61	***

Trichoptera abundance	WED 1000m	0.17	0.13	72.00	0.19	0.12	
Tree height	Farm type (mixed)	-0.30	0.14	23.20	0.04	-0.30	*
WED 1000m	Farm type (mixed)	0.32	0.17	23.95	0.07	0.33	
~~Tree height	~~WED 1000m	0.34	-	72.00	0.00	0.34	**

Diversity of insect orders

Diversity	Farm type (mixed)	-0.02	0.03	64.00	0.54	-0.08	
Diversity	Proportion cereals 500m	0.00	0.03	64.00	0.92	0.01	
Diversity	Crop div 250m	0.00	0.03	64.00	0.88	-0.02	
Diversity	Habitat diversity 250m	0.06	0.03	64.00	0.07	0.23	
Diversity	Tree height	-0.03	0.03	64.00	0.35	-0.12	
Diversity	Temperature	0.02	0.04	64.00	0.52	0.10	
Diversity	Temperature ^2	0.07	0.03	64.00	0.02	0.36	*
Tree height	Farm type (mixed)	-0.30	0.14	23.20	0.04	-0.30	*
Proportion cereals 500m	Farm type (mixed)	-0.32	0.16	23.78	0.05	-0.33	
Habitat diversity 250m	Farm type (mixed)	0.46	0.15	23.67	0.00	0.47	**
~~Habitat diversity 250m	~~Proportion cereals 500m	-0.47	-	72.00	0.00	-0.47	***

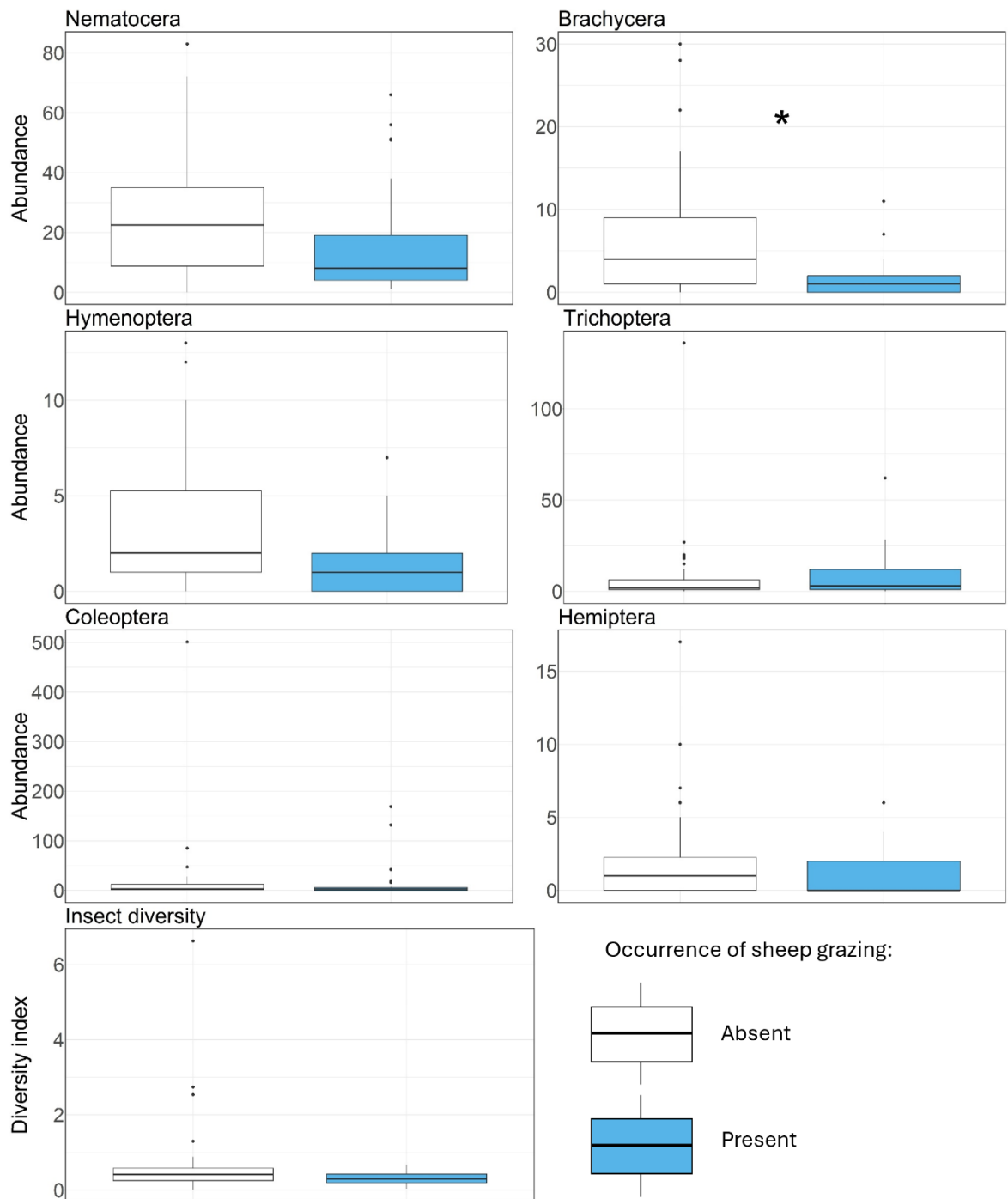


Figure S.3.3. Boxplots of insect abundance or diversity on farms with sheep grazing and without sheep grazing

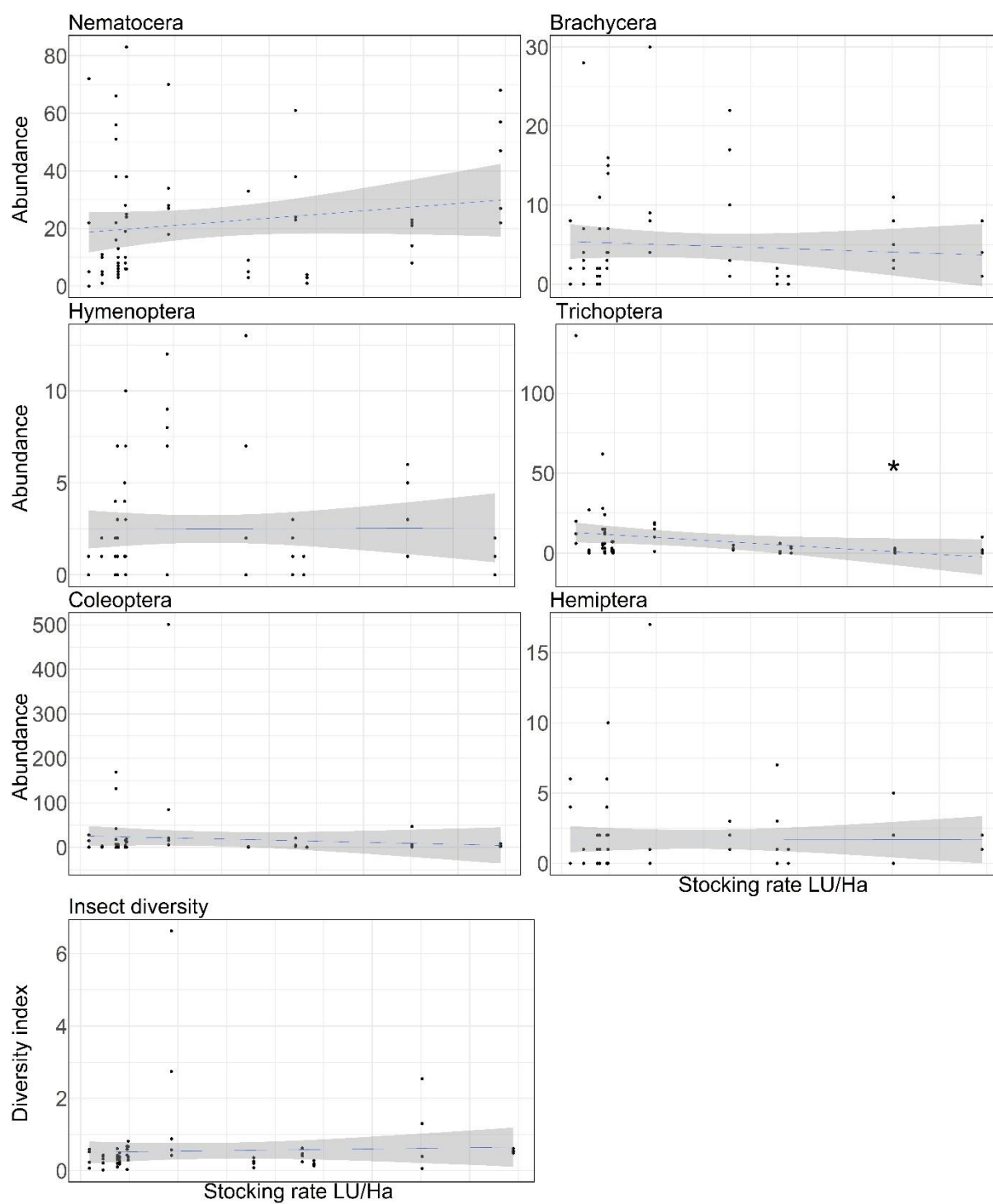


Figure S.3.4. Scatterplot of insect abundance at increasing stocking rates of cattle

Chapter 4: Contrasting effects of mixed farming on bats are mediated by local and landscape features and differ between seasons

Abstract

Homogenisation of agricultural landscapes, driven by intensive farming, is one of the key drivers of biodiversity decline in Europe. Whilst government schemes to address this have benefitted some species, they have been less successful for bats, which likely require a landscape-scale approach due to their high mobility. 'Mixed farming', where livestock are integrated into arable crop rotation, has been proposed as a landscape-scale approach to biodiversity loss and could benefit bats via increased diversity of foraging habitats, both spatially and temporally (e.g. in the autumn when arable fields are ploughed, pasture may provide an alternative source of insect prey). I investigated direct and indirect effects of mixed farming on bat activity and how these effects change between seasons. Bat activity was quantified on 26 farms in Scotland (UK) in summer 2022 and in autumn 2023 and 2024 using acoustic methods. On mixed farms, bats avoided arable fields in favour of grassland or woodland. Woodland edge density – which was higher on mixed than on arable farms – had a positive effect on occurrence of *Myotis* species. The activity of *Pipistrellus* and *Myotis* species was also positively associated with the height of treelines and hedgerows (which were marginally shorter on mixed farms than on arable farms). Thus, increasing the minimum hedgerow height set by current schemes would benefit these bat species. Bat responses differed between seasons, with habitat diversity becoming more important for *Pipistrellus pipistrellus* in the autumn, highlighting the importance of monitoring bats across the seasons to identify factors influencing bat activity.

4.1. Introduction

Agricultural land represents 40% of land use in Europe, the majority of which is managed intensively (European Union, 2025), characterised by homogenisation and specialisation of agricultural landscapes. Indeed, many farmers now specialise in one or two crops or in livestock production (Garrett et al., 2020), leading to areas of extensive crop monocultures or intensive livestock farming. Removal of woodlands, hedgerows and treelines has historically been associated with intensive farming and has added to landscape homogenisation (Downey et al., 2025). These woody features are important components of the agricultural landscape, providing shelter and landscape connectivity for a variety of taxonomic groups (Boutin et al., 2011a; Finch et al., 2020; Fuentes-Montemayor et al., 2013). Intensive agriculture is also associated with the use of synthetic inputs such as fertilisers, herbicides and pesticides which are known to be detrimental to insects (Dupont et al., 2018; Pisa et al., 2015a), with evidence of bioaccumulation of insecticides occurring in animals at higher trophic levels (Eng et al., 2019; Valdespino and Sosa, 2017). Thus, there is strong evidence that intensive agriculture is a key driver of biodiversity declines both globally (Outhwaite et al., 2022) and in the UK (Burns et al., 2016).

Bats are known to respond negatively to intensive farming, in particular to the loss of woody habitat and homogenisation of agricultural landscapes (Monck-Whipp et al., 2017; Put et al., 2019). In addition, bats are also vulnerable to bioaccumulation of pesticides (Zhao et al., 2020). Government financial incentives to increase wildlife on farms (Agri-Environment Schemes – AES) are beneficial for some taxa such as moths and beetles (Fuentes-Montemayor et al., 2011a; Thomas et al., 2002) but have had limited advantages for bats, with higher bat activity recorded on farms that were not implementing such schemes in comparison to those that were (Fuentes-Montemayor et al., 2011b), though hedgerows managed under AES can increase bat activity (Jérémy S.P.

Froidevaux et al., 2019). Due to their high mobility, bats may respond better to more landscape-scale changes in agricultural practices rather than field-scale schemes.

Mixed farming, where livestock are integrated into the crop rotation, has been suggested as a more sustainable approach than 'arable' farming (Jayasinghe et al., 2023; Lemaire et al., 2015). On a local scale, mixed farming can reduce the need for synthetic inputs that are harmful to insects via natural nutrient input from dung and natural weed-control from grazing (MacLaren et al., 2019; Schlegel et al., 2015). Grazing livestock can also directly influence bat activity by attracting or disturbing insect prey (Ancillotto et al., 2023; Downs and Sanderson, 2010). However, management of hedgerows on mixed farms may be different to arable farms: hedgerows on mixed farms are traditionally used to contain livestock and are usually subjected to regular trimming (Venturi et al., 2022). Furthermore, hedges or young trees may become damaged or altered from livestock browsing (Love et al., 2009; Schmitz et al., 2007). Linear woody features such as hedgerows and tree lines provide shelter and foraging for bats in otherwise very open agricultural landscapes (Finch et al., 2020), thus farming type may indirectly affect bats via hedgerow management practices.

At the landscape-scale, mixed farming may provide greater habitat diversity than arable farms, with a mix of cropland, pasture and woodland (that may often be retained as shelter for livestock). Indeed, bats have been found to avoid foraging over arable fields with some species preferring to forage over pasture or woodlands (Nicholls and Racey, 2006; Russ and Montgomery, 2002). Greater landscape diversity may become even more important for bats in the autumn. In fact, at a time of year when bats are feeding-up in preparation for hibernation, most arable fields will be left bare after harvest or ploughed over, reducing the abundance of insects (Thorbeck and Bilde, 2004), whilst pasture fields may continue to provide food resources and shelter for insects.

Thus, the effects of mixed farming on bats are likely to be complex and could be both indirect (via differences in local and landscape attributes) or direct and may change between seasons. Here, I assess the habitat preferences of foraging bats on mixed and arable farms. I also take a whole-system approach using structural equation modelling to disentangle the direct and indirect effects of mixed farming systems on bat activity or occurrence in North-East Scotland. Specifically, I address the following questions:

1. Do bat habitat preferences differ between arable and mixed farms?
2. Does mixed farming benefits bats, either directly or indirectly via landscape composition and configuration? If so, do these effects vary between peak activity (summer) and pre-hibernation (autumn) periods?
3. On mixed farms, is bat activity higher adjacent to pasture than in arable areas? And is this influenced by pasture management (e.g. livestock stocking rates)?

4.2. Methods

4.2.1. Site selection

Study sites were situated in Eastern Scotland (Figure S.4.1) between latitudes of 56.2 and 57.6 which is a highly agriculturally productive area of the UK, with fertile soils capable of growing a medium to wide range of crops (Scottish Government, 2009). I selected 13 mixed and 13 arable farms via contacts at Scotland's Rural College and using farmer recommendations. Here, I define 'arable' as a crop-only farm with no livestock integrated into the crop rotation. I define a 'mixed' farm as having grazing livestock integrated into the crop rotation, either through rotation of temporary grassland and/or by grazing cover crops or herbal leys. For simplicity, I limited mixed farms to those that kept cattle or cattle with some sheep grazing over the winter months. No other

livestock types were present on mixed farms. Whole-farm cattle stocking rate was calculated using the number of livestock units (LUs) and the total area of pasture available, with one LU approximately equivalent to one beef cow and calf (SAC Consulting, 2024b). I was unable to obtain accurate information on stocking rate of sheep for all farms where they were present, thus I noted presence or absence of sheep integrated into the rotation. Farms were situated in lowland areas with a mean altitude above sea level of 80 m (min: 9m, max: 190 m) and a mean size of 200 Ha (min 73 Ha, max 483 Ha).

4.2.2. Bat surveys

Two methods were used to survey bats: walked transects and static detectors. All surveys were conducted in a paired design: each mixed farm was paired with a nearby arable farm (mean distance: 9.5 km; min = 3 km; max = 16 km) and arms within the same pair were surveyed simultaneously to ensure similar weather conditions. All bat surveys were conducted on dry nights with a minimum temperature of 8 °C and a wind speed of less than 4 on the Beaufort scale (Fuentes-Montemayor et al., 2011b).

4.2.2.1. Walked transects

To assess habitat selection by bats in arable and mixed farms (Q1) foraging activity was recorded along transects once on each farm between June and July 2022 using a pair of hand-held Echo Meter 3 acoustic detectors (Wildlife Acoustics, 2011) with GPS unit to log the location of each bat pass recorded. The Echo Meters were set to 256kHz sample rate, high enough to detect the frequencies of all bat species found in Scotland. Detectors were held at elbow height and aimed upwards at a 45° angle from the ground. Transects were walked on 20 out of the 26 participating farms, with three pairs

unable to be surveyed due to logistical constraints. Surveys started 40 minutes after sunset to avoid peak emergence times (Fuentes-Montemayor et al., 2011b) and continued for a mean of 68 mins (min = 45 mins, max = 106 mins). Transects were designed to cover as many habitat types on each farm as possible, with a mean transect length of 3.3 km (min 1.6 km; max 4.5 km) and a mean walking pace of 3.1 km hr⁻¹. The same two surveyors were used for almost all farm pairs, alternating the farm type that was being surveyed by an individual. To avoid disturbance to crops and livestock, transects followed field edges which were often lined with hedgerows or lines of trees: mean percentage of transect that was adjacent to these woody features was similar between farm types at 48% for arable farms (min 31%; max 80%) and 47% for mixed farms (min 18%; max 74%).

4.2.2.2. Static detectors

To assess the direct and indirect effects of farm type on bat activity, mediated by local and landscape attributes (Q2), I carried out fixed-point surveys using Audiomoth acoustic recording devices (Hill et al., 2019) on the same pairs of farms as for walked transects, plus an additional three pairs (n = 26 farms). Two different survey periods were chosen: 28th June to 7th August 2022, which is during peak activity season for bat species in the north of the UK (Russ et al., 2003b) and prior to harvesting. I then returned to the same farms between 26th September and 10th October 2023, which corresponds to the pre-hibernation period reported for bats at similar latitudes (Frafjord, 2021b; Meier et al., 2022) and is after the main crop harvest period. Due to very cold and wet weather in autumn 2023, I was unable to survey all farms (total farms surveyed in 2023). I therefore returned to the remaining farms (n = 12) between 10th September 2024 and 4th October 2024. Static detectors were scheduled to begin recordings half an hour after sunset and stop recording half an hour before sunrise (settings are provided in Table S.4.1). To increase the

number of nights that could be recorded during longer autumn nights, I limited autumn recordings to two hours in the evening (starting half an hour after sunset) and two hours in the morning (ending half an hour before sunrise), as this is when bats have been found to be most active (Cel'uch and Kropil, 2008). This meant that recording time for summer nights (mean duration = 4.5 hours) were similar in length to autumn recordings. Recordings were for a mean of 5.5 nights during the summer period (min = 4, max = 7) and for a mean of 3.4 nights in the autumn (min = 1 (only one location), max = 7). During autumn deployment, temperature occasionally fell below 8 degrees Celsius (n = 7 nights), as measured by temperature loggers. These nights were subsequently removed prior to data analysis (n = 7 nights).

Three static detectors were deployed on each farm between two crop fields, hereafter called 'crop-crop' field margins (Figure 4.1). Since linear features are important for bats in agricultural landscapes (Finch et al., 2020) I placed static detectors along a hedgerow, line of trees or woodland strip (hereafter called 'woody features') approximately halfway along the field edge and at a height of 1.6m. A visual estimate of maximum woody feature height was noted within 15 m either side of the detector. To examine the effects of pasture presence and livestock management on bat activity (Q3), I placed an additional three detectors on mixed farms in crop fields (oriented towards the crop field) adjacent to pasture or 'crop-pasture' margins (Figure 4.1), resulting in three sampling points for every arable farm and six sampling points for every mixed farm.

a. Example of transect route



b. Experimental set-up of static detectors

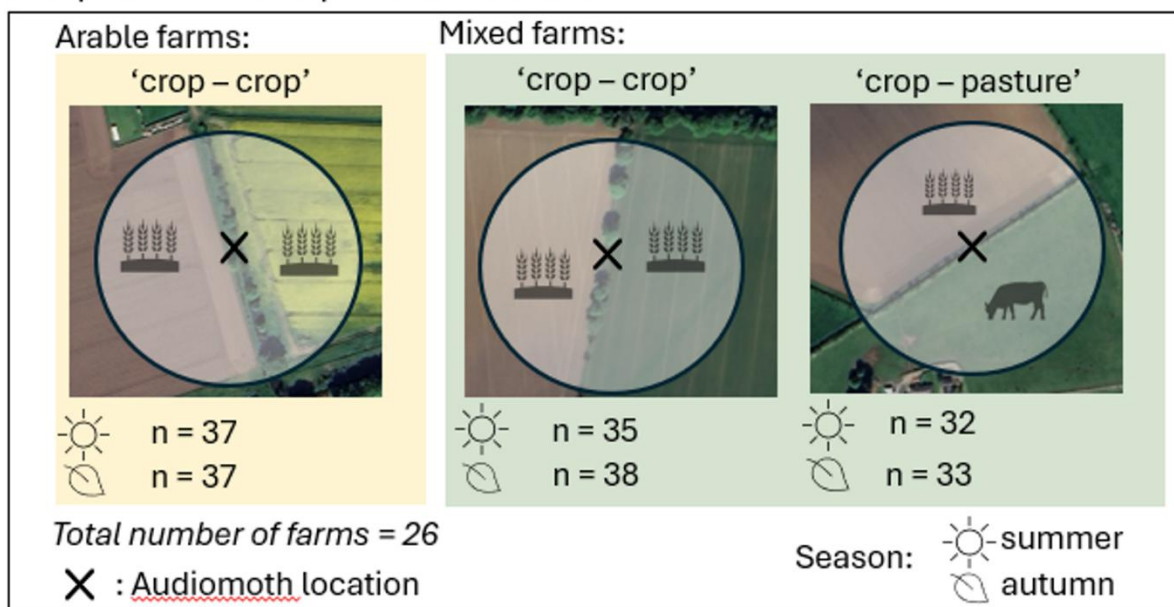


Figure 4.1: Set-up of static detectors (a) and example of transect route design (b). 'n' designates the total number of static detectors deployed in summer and autumn in each margin type ('crop-crop' on arable and mixed farms and 'crop-pasture' on mixed farms only).

4.2.3. Acoustic analysis

All acoustic files were split into 5 second files so that any continuous bat activity could be divided into five second passes, with one pass defined as at least two pulses (Azam et al., 2015; Millon et al., 2015) within a 5 second file. In the study area *Pipistrellus pipistrellus* and *Pipistrellus pygmaeus* are the most common species, with *Pipistrellus nathusii*, *Plecotus auritus*, *Myotis nattereri*, and *Myotis daubentonii* also present. I used Kaleidoscope (Wildlife Acoustic Inc, 2024) to carry out automatic identification of bats recorded on static detectors (settings are provided in Table S.4.2). Manual checks were then carried out on all files flagged by the software as *Myotis* spp. or *Plecotus auritus* as the software identifies these species with low accuracy (Rydell et al., 2017). All species from the genus *Myotis* were grouped as *Myotis* spp., as identification to species level for this genus is unreliable using acoustic methods (Rydell et al., 2017; Walters et al., 2012). Kaleidoscope's auto-identification feature cannot identify feeding buzzes, a rapid decrease in the distance between pulses that is associated with bats attempting to catch prey (Griffin et al., 1960). Therefore, I identified feeding buzzes manually on a subset of data (n = 40 nights across all farms). Feeding activity correlated positively with the number of bat passes for both *P. pipistrellus* (Pearson = 0.70, $P < 0.0001$) and *P. pygmaeus* (Pearson = 0.80 $P < 0.0001$, Figure. S.4.2) thus I used the number of passes as a proxy for bat feeding activity in all models.

4.2.4. Habitat analysis of transects

GPS locations of each pass were loaded into QGIS version 3.28.1. (QGIS Development Team, 2021). Habitat adjacent to transects was categorised as arable, pasture, woodland, buildings, water or semi-natural (scrub, heathland and semi-natural grassland combined) using a combination of farm maps provided by farmers and ground-truthing. Woodland habitat largely comprised mixed and broadleaf woodland, with riparian and coniferous woodland only representing 0.05% and 0.04% respectively of total transect proportion,

therefore all woodland types were grouped together for analysis. Each bat pass was then assigned to the adjacent habitat type (within 20 m of GPS location). Where there was more than one habitat type within 20 m of the bat pass, the pass was split across the number of habitat types present as in Fuentes-Montemayor et al., (2011b). To obtain a measure of habitat availability on each farm, I manually measured the total length of each habitat type adjacent to the transect in QGIS.

4.2.5. Landscape analysis

To obtain measures of landscape configuration and composition surrounding each static detector, I used The Centre for Ecology and Hydrology Land Cover Map (Marston et al., 2022) reclassified into biotypes (Table S.4.3). Buffers of 500, 1000, 1500, 2000, 2500 and 3000 m were created around each static detector location in QGIS. For each scale, I then used the *landscapemetrics* package (Hesselbarth et al., 2019) in R version 4.4.2. (R Core Team, 2023a) to extract landscape attributes that have been found in previous studies to be important for bats, including the proportion of arable, proportion of semi-natural (scrub and semi-natural grassland combined), woodland edge density, mean Euclidean nearest neighbour (ENN) for all woodland and Shannon's index of habitat diversity (Fuentes-Montemayor et al., 2011b, 2013; Walsh and Harris, 1996a) using biotypes (woodland, arable, grassland, freshwater, buildings, semi-natural, coastal; table S3). However, the mean proportion of semi-natural area was very low, even at larger scales (< 0.08 at the 1000 m scale) and was not considered in further analysis. In addition, I measured proximity of each static detector to the nearest freshwater body as well as proximity to the nearest building using OS MasterMaps® (Ordnance Survey GB, 2023).

4.2.6. Statistical analysis

4.2.6.1. Habitat preference on mixed and arable farms

To assess habitat preference of foraging bats (Q1) I used transect data to compare actual and expected use of habitat. This was conducted separately for *P. pipistrellus* and *P. pygmaeus* and for mixed and arable farms. There were insufficient passes of *Myotis* spp. for analysis of this group. The proportion of observed habitat use for each habitat type was calculated by dividing the number of bat passes assigned to each habitat type by the total number of bat passes. To calculate the proportion of expected use I assumed that habitat types were being used in proportion to their availability. Thus, I multiplied the proportion of each habitat available by the total number of bat passes recorded of each species. Passes associated with 'water' were removed from analysis as the expected number of passes was less than 5 (Neu et al., 1974). To assess the statistical significance of habitat selection or avoidance, I calculated simultaneous confidence intervals around each proportion of observed habitat use, following the same method as Glendell and Vaughan (2002), using Bailey's method with Bonferroni correction applied to avoid type II errors, with a significance level of $P < 0.05$. If the lower limit of the confidence interval was higher than the proportion of expected use, bats were deemed to be selecting for that habitat type. Conversely, if the upper limit of the confidence interval was below the proportion of expected use, bats were deemed to be avoiding that habitat type.

4.2.6.2. Structural equation modelling: exploring direct and indirect effects of farm type

To explore the direct and indirect effects of farm type on bats, mediated by local and landscape attributes (Q2) I used structural equation models (SEMs). SEMs are a multivariate technique to statistically test whether hypothesised

causal pathways (based on ecological theory) are supported by the observed data. For this analysis static detector data from crop–crop margins on arable and mixed farms and across both seasons was used (summer $n = 72$, autumn $n = 75$).

Prior to building structural equation models (SEMs), I evaluated which landscape features and at which spatial scales explained the greatest amount of variation in bat activity (and probability of occurrence for *Myotis* spp.). Generalised linear models (GLMs) were built, with number of passes for each *Pipistrelle* species as a response variable. Activity of *Myotis* spp. was low so occurrence was used as a response variable. Separate models were built for each landscape attribute at each spatial scale. I also modelled summer and autumn data separately to understand if there were any differences in the importance of landscape attributes and scales at different times of year. *P. pygmaeus* models were built using a Poisson distribution using the lme4 package (D Bates et al., 2015), whilst *P. pipistrellus* models showed overdispersion so I used a negative binomial distribution using the MASS package (Venables and Ripely, 2002). Occurrence of *Myotis* spp. was modelled using a binomial distribution. An offset to account for the number of nights recorded (log-transformed) was included in all GLMs. A pseudo r^2 value (for non-normally distributed data) was then calculated for each landscape variable at each different scale (Figure S.4.3.). Some landscape metrics were strongly correlated (Table S.4.4.). Thus, I selected one metric of landscape configuration (either woodland edge density or mean woodland ENN, whichever had the highest r^2 value (Figure S.4.3.)), plus one metric of habitat composition (either proportion of arable or habitat diversity index, again based on r^2 value) for inclusion in subsequent SEMs.

SEMs were built using the piecewiseSEM package (Lefcheck, 2016) which allows for the use of random effects and non-normal distributions. In addition to the landscape variables with the highest r^2 value, woody feature height was included in all models as this can influence bat activity (Jérémy S.P. Froidevaux

et al., 2019; Heim et al., 2016). For *P. pygmaeus* and *Myotis* spp. models I also included proximity to freshwater, since *P. pygmaeus* and *M. daubentonii* prefer foraging over water or riparian habitats (Bellamy and Altringham, 2015; Nicholls and Racey, 2006). For *P. pipistrellus* I included proximity to buildings since this species is known to make opportunistic use of buildings for roosting and foraging (Bellamy and Altringham, 2015; Hale et al., 2012). Finally, I included mean temperature at sunset to account for weather differences between deployment periods. To achieve model convergence, *P. pipistrellus* and *P. pygmaeus* count data was averaged to number of passes per night, log-transformed to achieve normality and modelled using a gaussian distribution. *Myotis* spp. occurrence (across all nights) was modelled as a binomial distribution. A random effect of 'site' was used in all models to account for multiple sample locations per site. For autumn models, a random effect of 'year' was initially included to account for sampling across two years. However, variances for year were very small so this was subsequently removed. In addition, continuous predictor variables in the *Myotis* spp. autumn model were scaled and centred around the mean to aid with model convergence. Each sub-model was checked for good model fit using the DHARMA package (Hartig, 2024). I then checked for missing pathways in SEMs using tests of directed separation (Shipley, 2000b). Pathways were subsequently included as correlated errors if they were found to be significant ($P < 0.05$) and overall SEM fit was verified using Fisher's C statistic (with a non-significant P value confirming that model is supported by the data).

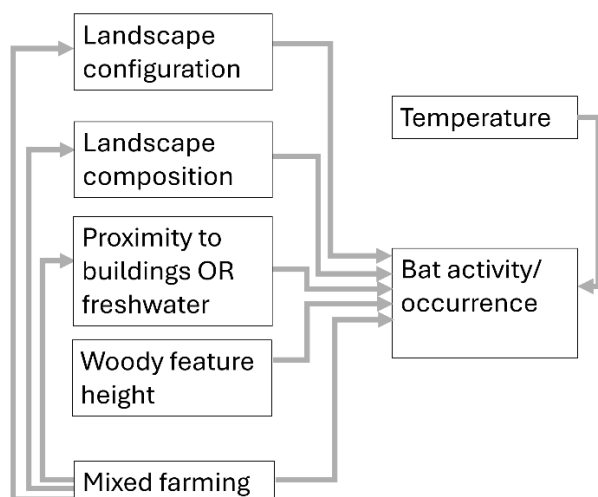


Figure 4.2: Metamodel showing hypothesized pathways between variables. Grey arrows indicate a hypothesized directional relationship that was modelled in SEMs.

4.2.6.3. Effects of pasture presence and management on mixed farms

To test the effect of pasture presence and management (i.e. livestock stocking rate and sheep presence) on bat activity (Q3), I used data collected on mixed farms. Separate generalized mixed effects models (GLMMs) were constructed for each bat species/group and for the summer and autumn sampling periods. All continuous predictor variables were scaled and centred around the mean. Predictor variables included in GLMMs were cattle stocking rate (for *P. pipistrellus* this was included as a quadratic effect as the relationship showed signs of non-linearity), occurrence of sheep on the farm and margin type ('crop-crop' or 'crop-pasture'). I also included woody feature height as this varied within each farm. 'Site' was included as random effect and 'number of nights' (log transformed) as an offset to account for unbalanced sampling. *Myotis* spp. Occurrence (across all nights) was modelled using a binomial distribution, whilst *P. pipistrellus* and *P. pygmaeus* activity was modelled as count data (total passes per detector across all nights) using a Poisson distribution. In autumn models, zero-inflation was detected for both *Pipistrellus* species. Therefore, zero-inflated models were built using the

glmmTMB package (Brooks et al., 2017). I then used corrected Akaike's Information Criterion (AICc) for small sample size to compare the zero inflated model with non-zero inflated Poisson and non-zero inflated negative binomial models (Bolker et al., 2024). The model with the lowest AICc was retained as the final model. All GLMMs were checked for goodness of fit using the DHARMA package.

4.3. Results

Across a total of 67 km of walked transects and 20 farms I recorded 485 *P. pipistrellus* passes, 486 *P. pygmaeus* passes and 10 *Myotis* spp. passes. *Pipistrellus pygmaeus* was recorded on all farms, whilst *P. pipistrellus* was recorded on all but two farms. However, *Myotis* spp. was only recorded at five sites (two arable and three mixed farms) and no other bat species were recorded during transect surveys.

Across all static detectors deployed during the summer months (n = 113 across 26 farms), I recorded a total of 72, 407 *P. pipistrellus* passes and 128, 419 *P. pygmaeus* passes. During autumn deployment (n = 116) a total of 8,320 *P. pipistrellus* and 28, 856 *P. pygmaeus* passes were recorded across all detectors. *Myotis* spp. was recorded on 55 detectors in the summer and 19 detectors in the autumn. *Plecotus auritus* was confirmed on a small number of recordings (n = 10) but was not sufficient for statistical analysis.

4.3.1. Habitat preferences of foraging bats in mixed and arable farms

P. pipistrellus habitat selection differed between the two farm types, with the species selecting for grassland and avoiding arable fields on mixed farms but not on arable farms. *P. pipistrellus* selected for farmland buildings on both

farm types, with observed *P. pipistrellus* activity around twice as high than expected (Table S.4.5). *Pipistrellus pygmaeus* showed no habitat preference or avoidance on arable farms but strongly selected for woodland (with observed passes almost twice as high as expected). *Pipistrellus pygmaeus* also strongly avoided arable fields on mixed farms (with observed passes half that of the expected value) and slightly avoided buildings on both farm types (Figure 4.3).

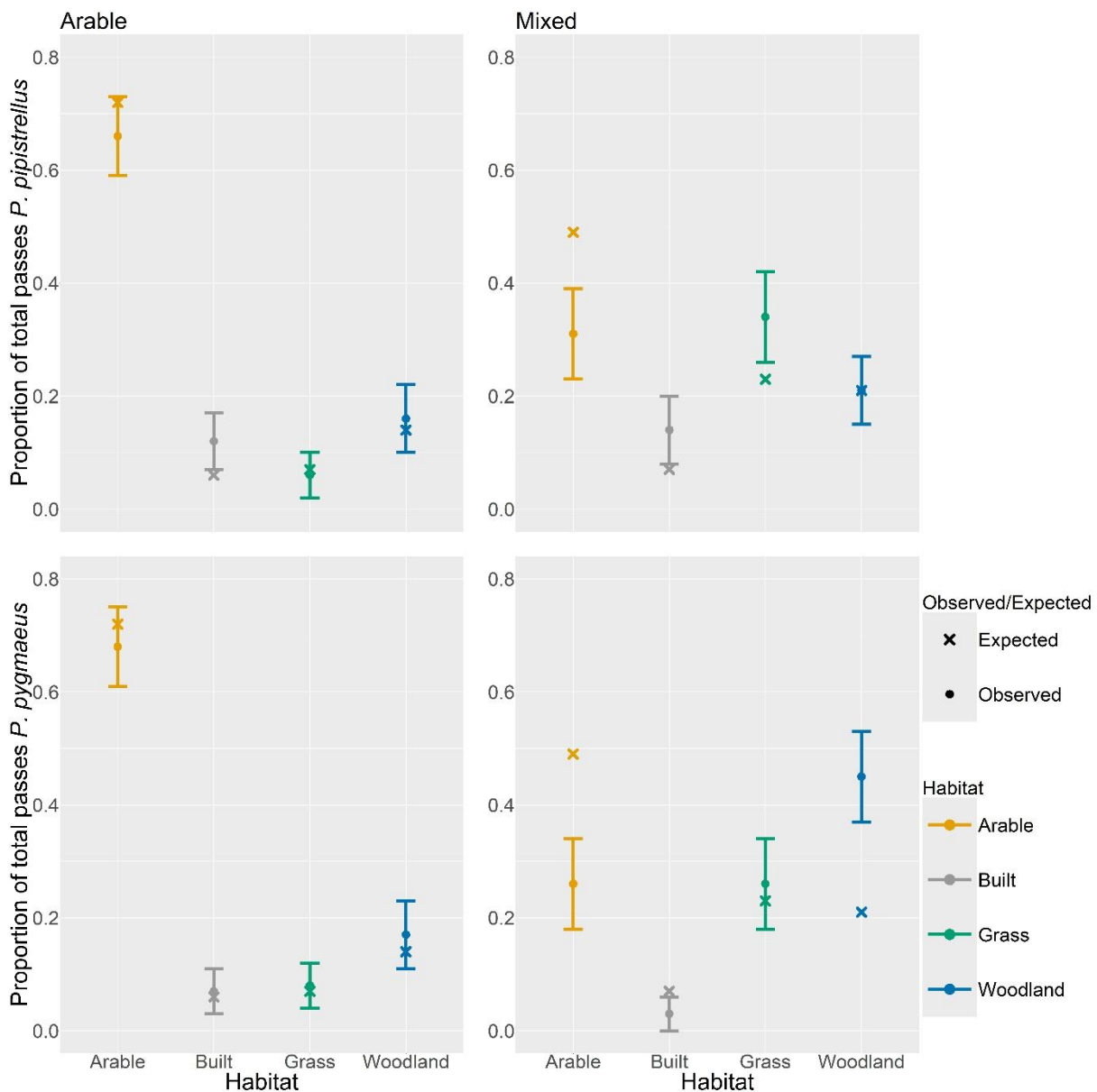


Figure 4.3: Habitat selection of *P. pipistrellus* on arable (a) and mixed (b) farms and of *P. pygmaeus* on arable (c) and mixed (d) farms. The proportion of expected passes given the proportion of habitat available is shown with an 'x', whilst points and associated error bars show the proportion of observed passes with 95% confidence intervals. Where the proportion of expected passes lies above error bars this is interpreted as habitat avoidance, whilst habitat selection is deemed to occur where the proportion of expected passes lies below the error bars.

4.3.2. Effects of mixed farming, landscape and local attributes on bats

Mixed farms had significantly higher woodland edge density than arable farms at larger scales of 1500 m and 2500 m (Figure 4.4). Habitat diversity was also significantly higher on mixed farms but only at the 500 m scale. Mixed farming had lower mean ENN for woodland patches at scales of 1000 and 1500 m, meaning that woodland patches tended to be closer together on mixed farms than on arable farms (Figure 4.4), though this was marginally non-significant (P value greater than 0.05 but less than 0.1). Woody feature height tended to be lower on mixed farms though this effect was also marginal, only explained 6% of the variation in woody feature height and was not significant in autumn models, for which the subset of farms sampled differed slightly to that in summer.

P. pipistrellus activity was unaffected by landscape composition or configuration in the summer months. Distance from buildings and local woody features were the only significant predictors of *P. pipistrellus* summer activity. Activity was higher closer to buildings, declining by 15 % with every 50 m increase in distance from buildings. Local-scale woody features were also important, with an increase of two meters in woody feature height associated with an increase of 12 % *P. pipistrellus* activity. As woody feature height was marginally lower on mixed farms, this resulted in an overall negative effect of mixed farming on *P. pipistrellus*. In the autumn, woody feature height and distance from buildings remained significant predictors of *P. pipistrellus* activity, an increase of 2 m in woody feature height was associated with an increase of 20 % *P. pipistrellus* activity, whilst activity declined by 25% with every 50 m increase in distance from buildings. Additionally, *P. pipistrellus* activity was marginally (P = 0.06) higher in landscapes with higher habitat diversity within 2000 m in autumn.

Pipistrellus. pygmaeus responded to both local and landscape features in the summer months. Woodland edge density at the 500 m scale positively

influenced *P. pygmaeus* by increasing activity by 15 % with every additional 10 m of woodland edge per hectare. On a local scale, an increase in woody feature height of 2 m was associated with an increase in activity of 11% in the summer months, leading to a marginal negative effect of mixed farming. This positive effect of woody feature height persisted in the autumn, with every 2 m increase in woody feature height associated with an increase of 24 % activity, however, this effect was not associated with farm type. I did not detect any effects of landscape composition or configuration on this species during the autumn.

In summer, *Myotis* spp. responded positively to increasing woodland edge density at the 1500 m scale, with an increase of 10 m of woodland per hectare increasing the chance of recording *Myotis* spp. by 39%. I also detected a marginally non-significant positive effect of woody feature height (marginally shorter in mixed farms). An increase in woody feature height of 2 m was associated with an increased chance of recording *Myotis* spp. of 12%. Overall, the positive effect of mixed farming on *Myotis* spp. via woodland edge density outweighed the (marginal) negative effect of mixed farming mediated by lower woody feature height. No effects of farming type, local or landscape features were detected for *Myotis* spp. in autumn.

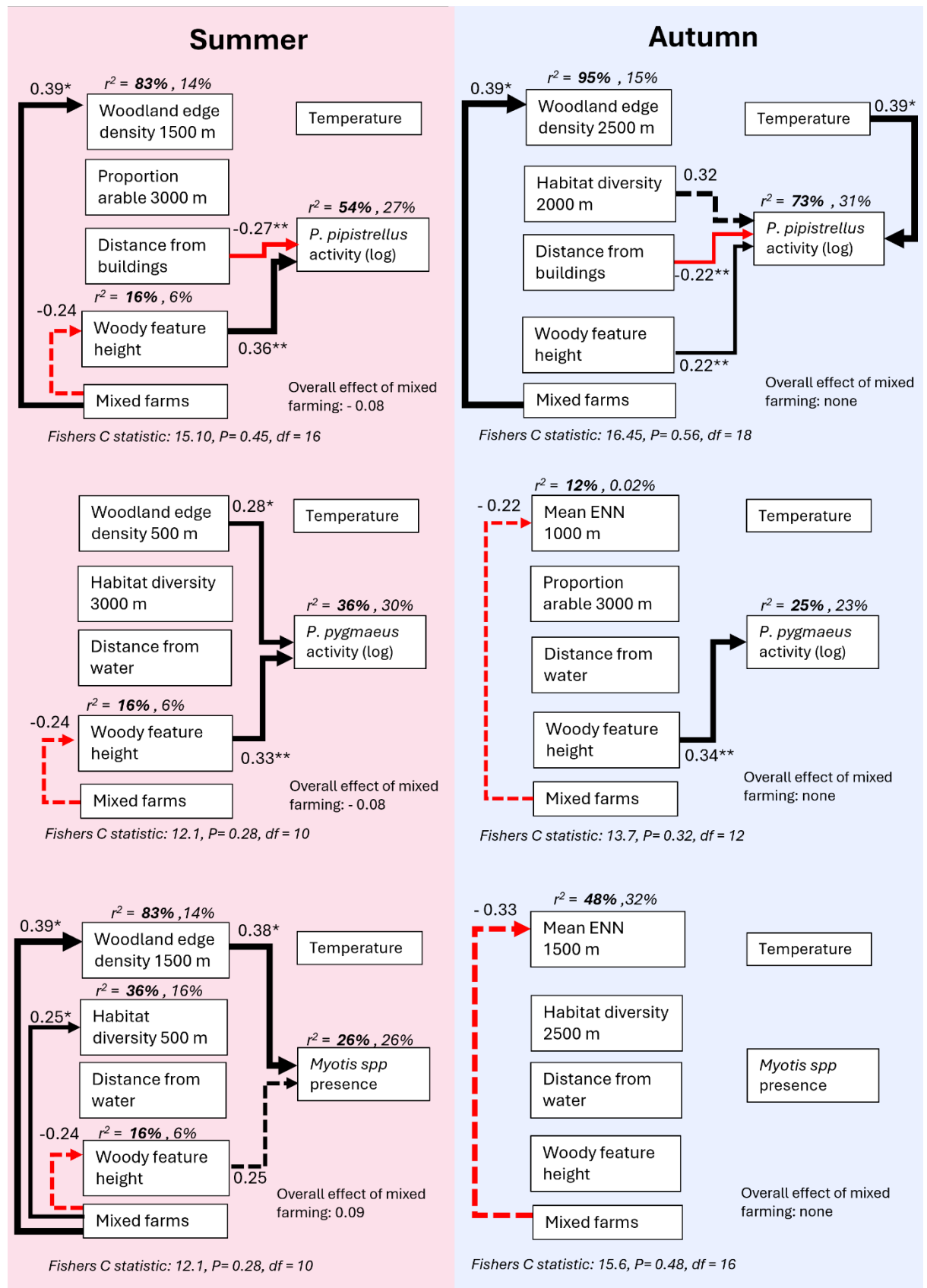


Figure 4.4: SEM path diagrams for *P. pipistrellus*, *P. pygmaeus* and *Myotis* spp. for summer (pink) and autumn (blue). Black arrows show a positive effect whilst red arrows show a negative effect. Full arrows show a significant effect ($P < 0.05$) and dashed arrows show a marginal effect ($P > 0.05 < 0.1$). Standardized coefficients for each pathway are given with significance stars associated (significance codes: '*' $p \leq 0.05$, '**' $p \leq 0.01$, '***' $p \leq 0.001$). Conditional r^2 (in bold-italic) and marginal r^2 (italic) values are given

above each variable with significant or marginal pathways. Correlated errors and all *p*-values are given in table S.4.6.

4.3.3. Effects of pasture presence and livestock management

Within mixed farms, there were no significant differences in bat activity between crop-crop or crop-pasture margins for *P. pipistrellus*, *P. pygmaeus* or *Myotis* spp. either during the summer months or autumn (Figure. S.4.4). *P. pipistrellus* activity had a non-linear significant relationship with cattle stocking rate in autumn but not in the summer, with lower activity associated with farms with less than 1.5 LU Ha⁻¹ (Figure 4.5b.). *P. pygmaeus* activity levels were positively and linearly associated with cattle stocking rate in the autumn but not in the summer (Figure. 4.5c and 4.5d), with a small increase of 0.5 *P. pygmaeus* passes per night associated with an increase of 1 LU Ha⁻¹ (the equivalent of one additional cow and calf per hectare). Autumn *P. pygmaeus* activity was also significantly higher on farms where sheep were present (+ 1.7 passes per night; *P* = 0.0004). I found a marginally non-significant positive effect of cattle stocking rate on *Myotis* spp. occurrence in the summer. Overall GLMMs explained a reasonable amount of the variation in bat activity or occurrence on mixed farms ranging from 26% to 69% (Table S.4.7.).

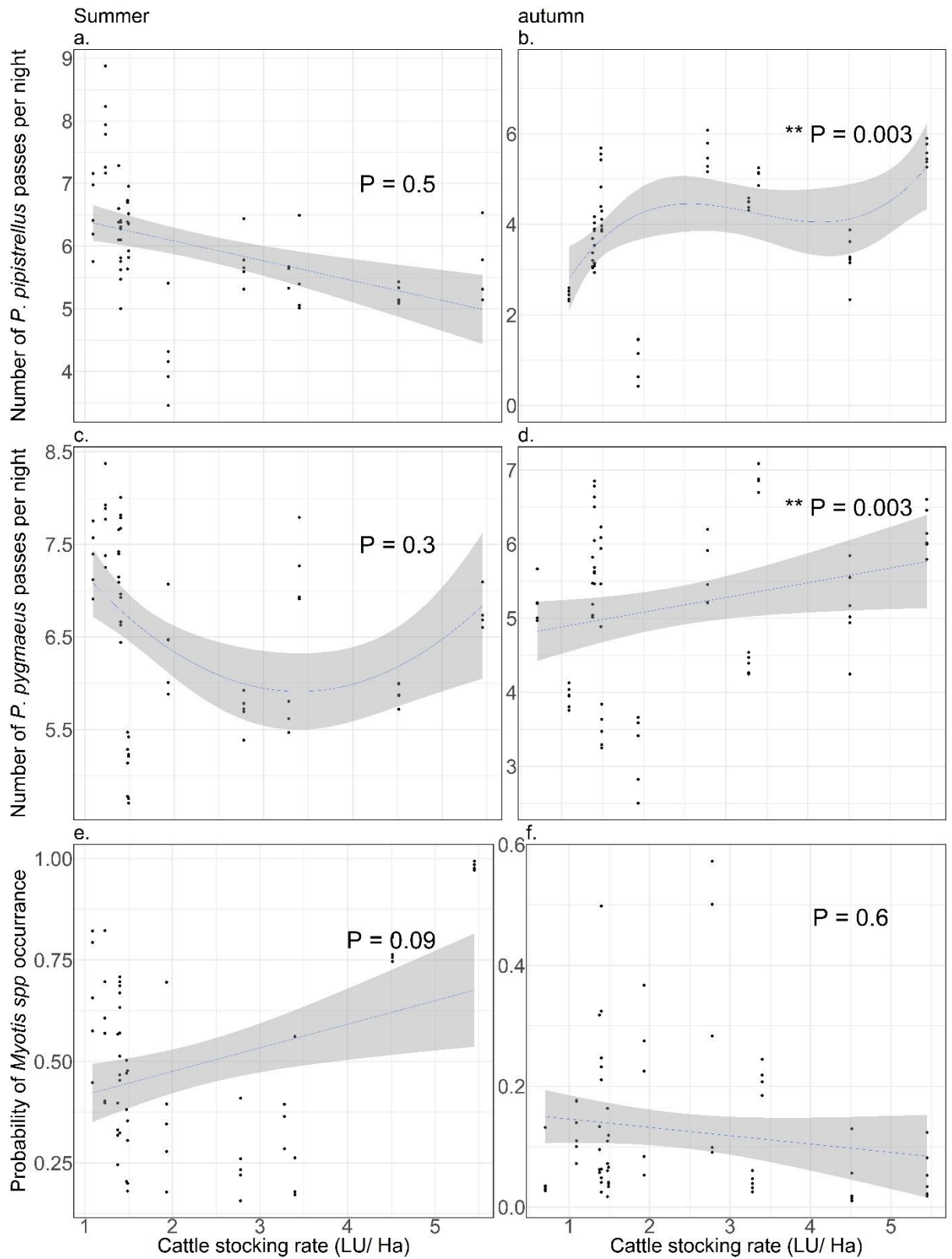


Figure 4.5. Predicted change in *P. pipistrellus* and *P. pygmaeus* activity and *Myotis* occurrence with cattle stocking rate. Significance codes: '***' $p \leq 0.001$; '**' $p \leq 0.01$; '*' $p \leq 0.05$, '(.)' $p \leq 0.1$. label panels.

4.4. Discussion

To my knowledge, this is the first time that the impacts of mixed farming on bat foraging activity and habitat preferences have been investigated. I found that habitat selection of bats differed between farm type, with bats preferring woodland or grassland habitat on mixed farms but not on arable farms. In my whole-system approach I found no direct benefits of mixed farming compared to arable farming. Instead, bat activity or occurrence was influenced by local and /or landscape attributes. However, I found differences in landscape attributes of mixed and arable farms, which resulted in a higher probability of *Myotis* spp. occurrence in mixed farms (which have higher woodland edge density). In addition, I found that the effects of mixed farming and livestock management on bat activity differed between seasons, highlighting the importance of monitoring bat response at different times of year.

4.4.1. Bat habitat preferences differ between mixed and arable farms

I detected no significant habitat selection or avoidance by bats on arable farms. In contrast, both *P. pipistrellus* and *P. pygmaeus* avoided arable fields on mixed farms (but not on arable farms), with *P. pipistrellus* selecting for grassland and *P. pygmaeus* selecting for woodland in mixed farms. The avoidance of arable and selection of grassland and woodland has been found in other studies (Nicholls and Racey, 2006; Russ and Montgomery, 2002) suggesting that whilst both species can forage over arable land, they avoid it and show preference for other habitats when these are available, potentially due to lower insect abundances in arable fields compared with pasture or woodland (Evans et al., 2007; Garrett et al., 2022a). These differing habitat preferences between farm types could also be driven by differences in the wider landscape (section 4.3.).

Preference of farm buildings by *P. pipistrellus* on both farm types shows that this is an important resource in the agricultural matrix for this species. Some studies have found that livestock sheds can provide insect resources for bats (Dietz et al., 2013; Nosal et al., 2019). However, the selection of buildings by *P. pipistrellus* on both farm types in my study suggest that buildings are important regardless of livestock presence, likely by providing sheltered areas for insects and foraging bats in otherwise very open agricultural landscapes or important roosting sites for *P. pipistrellus*. Although my sampling design avoided peak emergence times, *P. pipistrellus* is known to increase regularity of feeding bouts during lactation (Davidson-Watts and Jones, 2006b), which coincides with the survey period for transects (June – July) and could explain higher activity around buildings even after peak emergence.

4.4.2. Importance of landscape composition and configuration

I found significant associations between farming type and landscape composition and configuration. Mixed farming was associated with higher woodland edge density at larger scales (1500 and 2500 m) but not at smaller scales (500 m), and higher habitat diversity at smaller scales (500 m). It is possible that the presence of pasture habitat on mixed farms could contribute to higher habitat diversity on mixed farms at smaller scales (500 m). However, woodland configuration associated with mixed farming at larger scales (but not smaller scales) suggests that this is unlikely to be a causal effect of mixed farming, particularly given that mean farm size was only 200 Ha.

P. pipistrellus activity was not influenced by landscape composition or configuration during the summer months. However, there was more activity in landscapes with higher habitat diversity in the autumn. The higher abundance of insects between June and July could mean that this generalist species isn't particularly affected by habitat configuration or composition during the

summer months when food availability is high. However, in the autumn when crops have been harvested and temperatures drop, insects become less active (Welti et al., 2022) and may be concentrated in certain habitat types such as woodlands (Rigot et al., 2013). The positive effect of habitat diversity on *P. pipistrellus* activity found only in the autumn shows that this species can make use of a variety of habitats when insects are scarce. My findings that the activity of *P. pipistrellus* increased closer to buildings in both summer and autumn, agrees with findings from my transect data that farmland buildings are an important landscape feature for this species. Whilst use of buildings by *P. pipistrellus* for roosting is well known (Hale et al., 2012), to my knowledge this is the first time that their importance as foraging features in homogenous agricultural landscapes has been found.

Woodland edge density was important for both specialist species (*P. pygmaeus* and *Myotis* spp.) during the summer months at scales similar to the known foraging/colony ranges for these species (Encarna o et al., 2006; Mordue et al., 2023; Nicholls and Racey, 2006). The positive effects of woodland edge density for *P. pygmaeus* and *Myotis* spp. corresponds with findings from Davidson-Watts and Jones (2006) and Nicholls and Racey (2006) and could be in part due to preferences for roosting in woodland for *P. pygmaeus* or near water bodies that are often associated with woodland for *M. daubentonii* (Encarna o et al., 2006; Lu an et al., 2009). In addition, these species are edge-adapted, preferring to forage along woodland edges (Walsh and Harris, 1996b). Woodland configuration (as measured by mean woodland ENN) had no significant effect on these two specialist species in the autumn. *Myotis* spp. presence was very low in the autumn, only being recorded on 19 out of 116 static detectors and with no effect of landscape composition or configuration found. This may have been influenced by *M. daubentonii* entering the hibernation period before the end of my survey period (Meier et al., 2022). Thus, presence of *Myotis* spp. in September and October may be more related to the location of suitable hibernacula rather than any landscape variables.

4.4.3. Importance of local woody features

Local scale woody features were significant predictors of *P. pipistrellus* in both summer and autumn months. Activity of both Pipistrelle species and probability of occurrence of *Myotis* spp. increased with woody feature height. Whilst this effect has been seen for other bat species (Jérémy S.P. Froidevaux et al., 2019) and trees incorporated into hedgerows have been found to increase *P. pygmaeus* activity (Boughey et al., 2011; Finch et al., 2020), to my knowledge, this is the first time the positive effect of increasing hedgerow height has been found for *P. pipistrellus* and *Myotis* spp.. Whilst current agricultural policies in Scotland support the retention of trees within hedgerows, management prescriptions that aim to manage and restore hedgerows for wildlife (Scottish Government, 2023) encourage regular trimming (every 2 – 3 years) and set a very low minimum hedgerow height (1.5 m) which is unlikely to be beneficial for bats, given that in my study peak activity was recorded adjacent to woody features that were 15m high for *P. pipistrellus* and 25 m for *P. pygmaeus*. Though mixed farms in my study had marginally lower hedgerows/ treelines in comparison to arable farms, farm type explained a very low amount of the variation in woody feature height ($r^2 = 6\%$) and the effect was not significant in autumn models (likely due to changing the location of some detectors between summer and autumn sampling). Marginally lower woody features on mixed farms could be due to management of hedgerows to contain livestock or hedgerow height may even be reduced by browsing livestock in adjacent fields. Regardless of the drivers of woody feature height, taller hedgerows and treelines are likely to benefit both *Pipistrellus* spp. and *Myotis* spp. on both arable and mixed farms.

4.4.4. Stocking rate is more important than pasture presence for bat activity on mixed farms

I found no difference in bat activity between crop-crop and crop-pasture margins. Whilst this lack of difference is expected during the summer months when insects are abundant, it is surprising that I found no effect in the autumn when arable fields are generally bare following harvest and pasture could provide a more permanent habitat for insects. The lack of higher bat activity adjacent to pasture could be because livestock were not present in all pasture fields during autumn surveys (only eight out of the 31 crop-pasture margins where detectors were placed contained cattle at time of surveys) as this is the time of year when cattle are moved into barns in my study area. This is consistent with findings from Downs and Sanderson (2016) where bat activity was higher over fields containing cattle than over empty pasture where dung was present. Therefore, it could be that the pasture itself does not provide an important insect resource in the autumn but that the presence of livestock is more important. Indeed, I found a positive effect of cattle stocking rate on both Pipistrelle species in the autumn (non-linear for *P. pipistrellus*, plateauing at around 2 LUs) and a positive effect of sheep presence on *P. pygmaeus* in the autumn, though the increase in bat activity associated with stocking rate was very small for both Pipistrelle species. Evidence of bats feeding around livestock and a non-linear association has been reported by (Ancillotto et al., 2017). My findings of increasing activity with higher stocking rates only in the autumn suggest that higher livestock numbers may be providing small additional insect resources on mixed farms during the pre-hibernation period.

4.4.5. Management recommendations

I investigated whether mixed farming is beneficial for foraging bats in comparison to arable farming. Mixed farming did not directly benefit bats in my study, although it was associated with landscape composition and

configuration attributes that are beneficial for bats, such as higher woodland edge density, woodland patches closer together and higher habitat diversity. Greater woodland edge density increased activity of all three bat species/groups and increasing woodland on farms regardless of farm type is likely to be beneficial for foraging bats. In addition, Pipistrelle bats avoided arable fields in favour of woodland and grassland where these were available on mixed farms. *Pipistrellus pipistrellus* selected for farmland buildings, which also provided important foraging grounds across the seasons. Policies that encourage bat-friendly farmland buildings could further enhance the use of these important features for *P. pipistrellus*. Positive effects of habitat diversity on *P. pipistrellus* were only apparent in the autumn, suggesting that this generalist species is able to make use of a variety of habitat types at a time of year when insects are scarce. Future agricultural policies that aim to benefit bats at a landscape scale should take into account habitat requirements at different times of year. Higher farm-level cattle stocking rates were only associated with a slight increase in Pipistrelle activity in the autumn, suggesting that greater numbers of livestock are only providing a small benefit to bats, potentially via additional insect resource at a time when insects are scarcer. Taller woody features increased foraging activity or occurrence of all species/groups studied. Increasing the minimum hedgerow height requirement for future Agri-Environment Schemes could encourage greater foraging activity of a variety of bat species on farms.

Acknowledgements

I would like to thank all landowners for allowing data collection to take place on their farms, with special thanks to Charlotte Wood for assisting with fieldwork. This project was fully funded by Scotland's Rural College (SRUC).

Supplementary material chapter 4

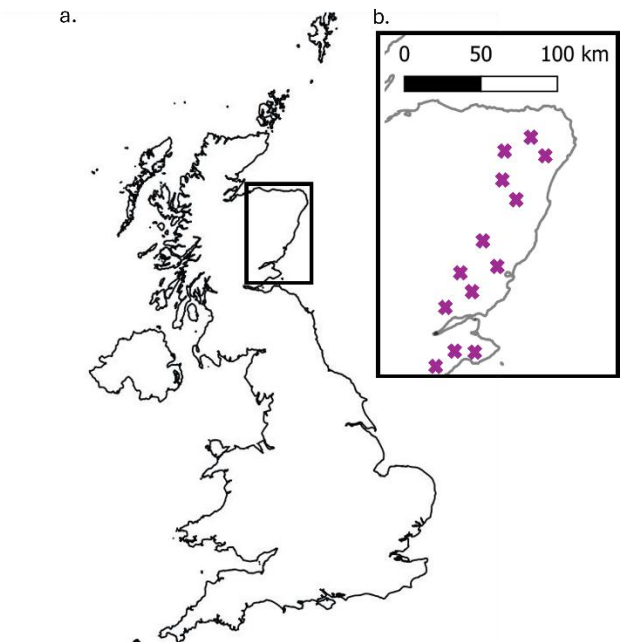


Figure S.4.1: Map showing a. location of study area and b. approximate locations of study sites. Pairs of sites are designated by a purple 'x', with each farm within a pair no more than 16km apart.

Table S.4.1: Settings used to configure Audiomoths

Setting	Value
Firmware	AudioMoth-Firmware-Basic (1.8.1)
Sample rate (Hz)	250000
Gain	Low-Medium
Sleep duration (s)	0
Recording duration (s)	300
Filter	none
Trigger type	Amplitude
Threshold setting	1%
Minimum trigger duration (s)	2
Disable 48Hz DC blocking filter	No
Enable energy saver mode	No
Enable low gain range	No

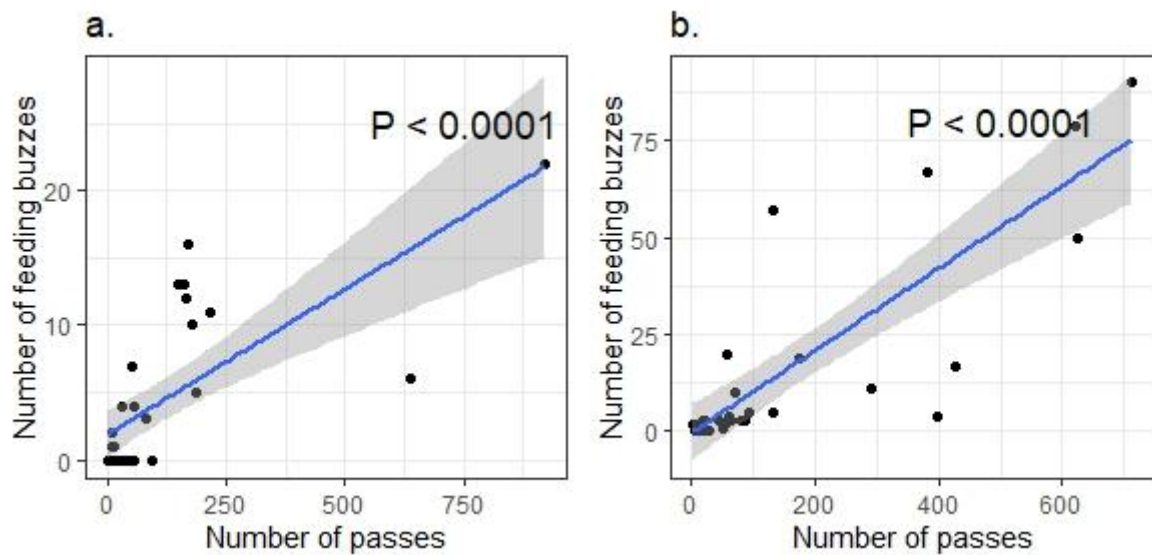


Figure S.4.2: Plots showing the relationship between a. *P. pygmaeus* activity and feeding buzzes and b. *P. pipistrellus* activity and feeding buzzes

Table S.4.2: Kaleidoscope settings

Setting	Value/ options
Spilt to max duration	5 seconds
Move noise to subfolder	yes
Time expansion factor	1
Compression	none
Classifiers	Species selected for autoidentification: - <i>Pipistrellus pipistrellus</i> - <i>Pipistrellus pygmaeus</i> - <i>Pipistrellus nathusii</i> - <i>Plecotus auritus</i> - <i>Nyctalus noctula</i> - <i>Nyctalus leisleri</i> - <i>Myotis daubentonii</i> - <i>Myotis nattereri</i> - <i>Myotis mystacinus</i>

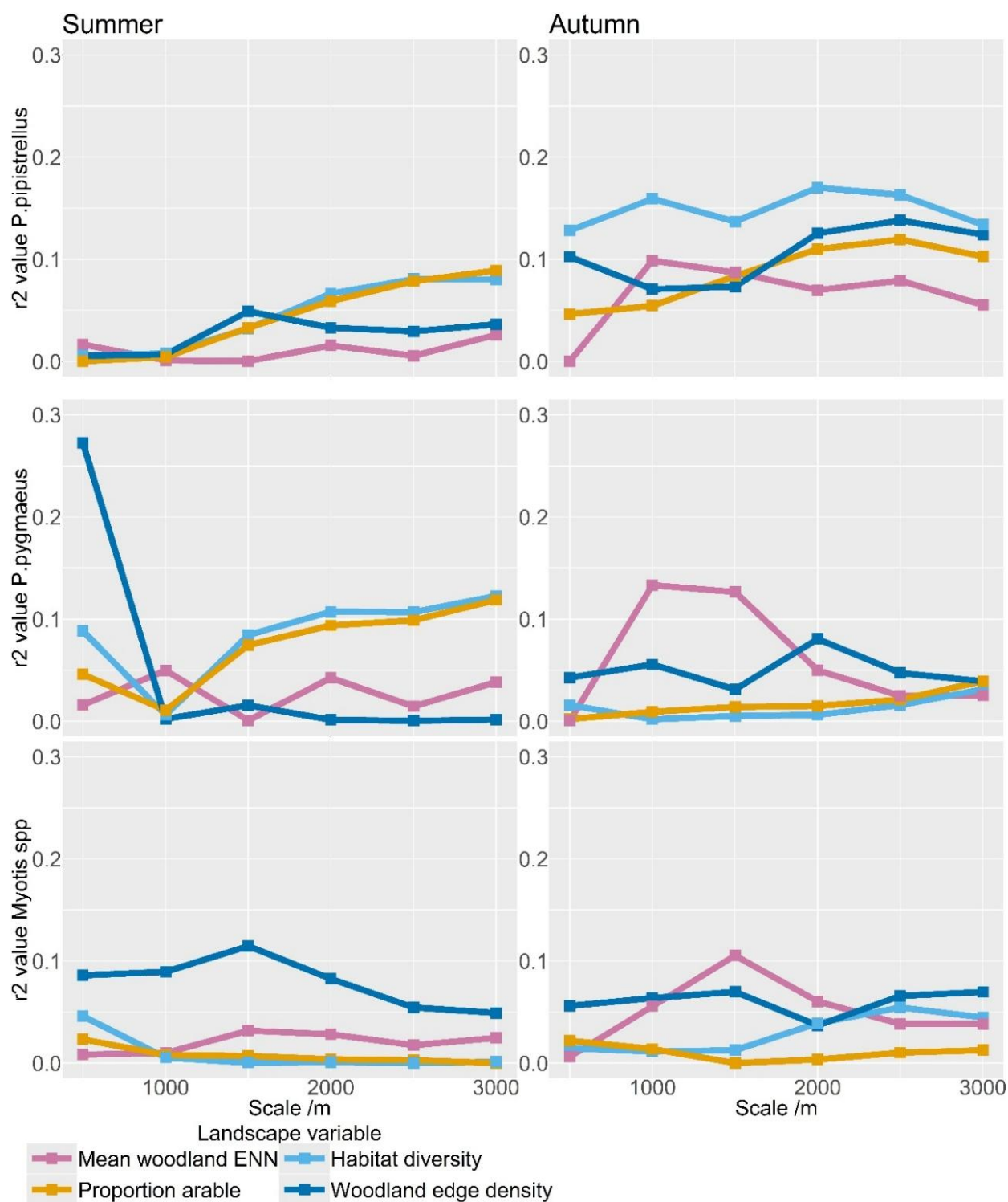


Figure S.4.3. plots showing r^2 values for each landscape variable across different scales and between season for *P. pipistrellus*, *P. pygmaeus* and *Myotis spp.*

UKCEH Land Cover Class	Assigned category
Deciduous woodland	Woodland
Coniferous woodland	Woodland
Arable	Arable
Improved grassland	Improved grassland
Neutral grassland	Semi-natural
Calcareous grassland	Semi-natural
Acid grassland	Semi-natural
Fen	Semi-natural
Heather	Semi-natural
Heather grassland	Semi-natural
Bog	Semi-natural
Inland rock	Semi-natural
Saltwater	Coastal
Freshwater	Freshwater
Supralittoral rock	Coastal
Supralittoral sediment	Coastal
Littoral rock	Coastal
Littoral sediment	Coastal
Saltmarsh	Coastal
Urban	Built
Suburban	Built

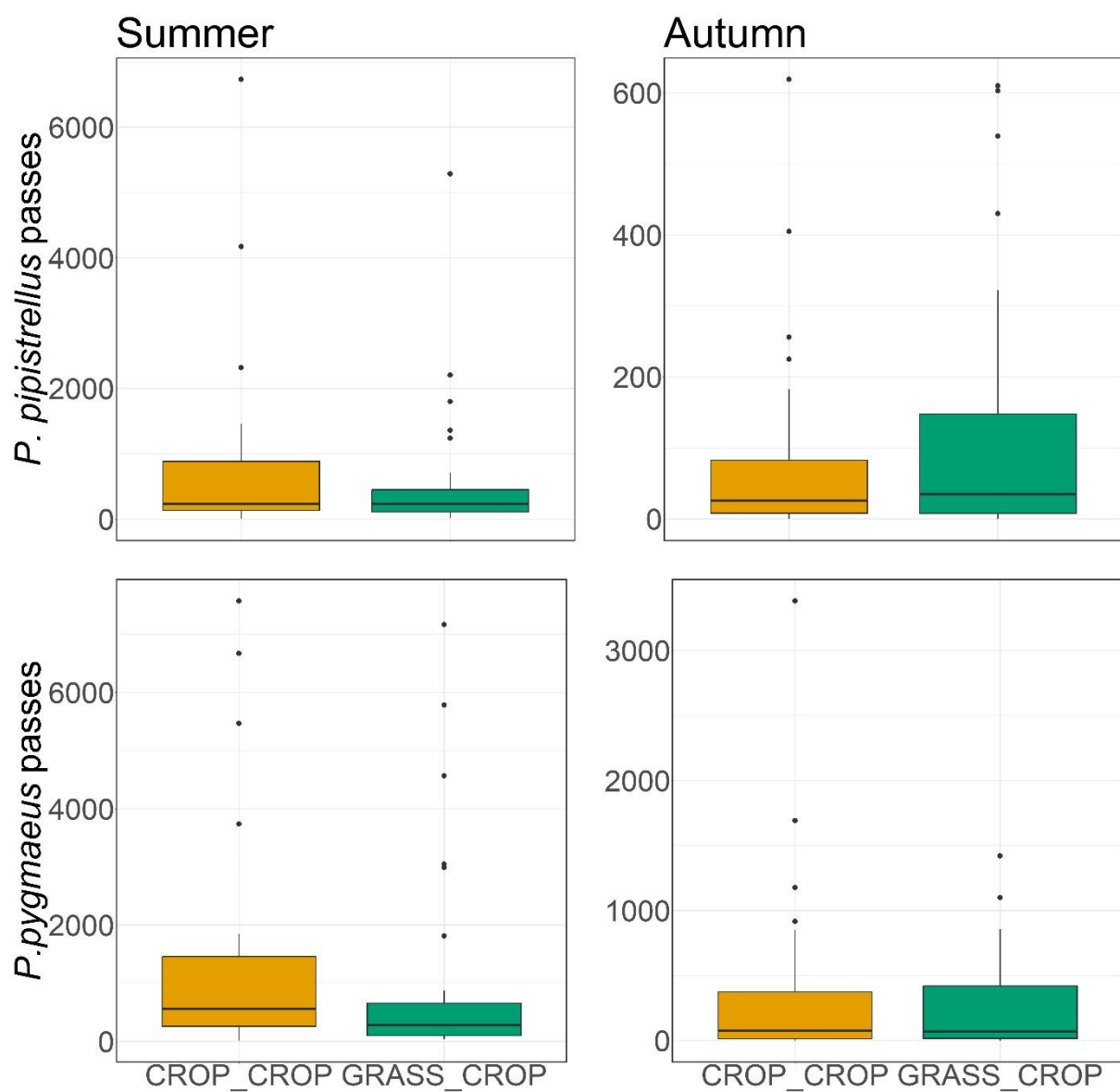


Figure S.4.4: boxplots showing the number of *Pipistrelle* passes on mixed farms associated with crop-crop (in yellow) and grass-crop (in green) margins across the two seasons (summer/ autumn).

Table S.4.4. Correlation matrix of landscape and local variables for bat models

	Tree height	Temperature	Distance from water	ENN 500m	ENN 1000m	ENN 1500m	ENN 2000m	ENN 2500m	ENN 3000m	WED 500m	WED 1000m	WED 1500m	WED 2000m	WED 2500m	WED 3000m	Habitat diversity 500m	Habitat diversity 1000m	Habitat diversity 1500m	Habitat diversity 2000m	Habitat diversity 2500m	Habitat diversity 3000m	% arable 500m	% arable 1000m	% arable 1500m	% arable 2000m
Tree height	1	-0.19	-0.13	0.04	0.23	0.25	-0.14	-0.13	0.01	0.28	0	-0.1	0.05	0.02	0.01	0.05	-0.12	-0.2	-0.19	0.22	0.25	0	0.08	0.13	0.11
Temperature	-0.19	1	-0.2	0.06	0.04	0.09	0.11	0.09	0.06	0.06	0.16	0.2	0	0	0.02	0.23	0.2	0.21	0.27	0.26	0.23	0.23	-0.31	0.33	0.36
Distance from water	-0.13	-0.2	1	0.07	0.05	0.02	0.09	-0.2	-0.2	-0.21	0.03	0.07	0.16	0.19	0.2	-0.19	0.02	0.12	0.16	0.13	0.08	0.03	0.05	0.04	0.04
ENN ^a 500m	0.04	0.06	0.07	1	0.04	0.05	0.07	0	0.02	-0.27	-0.17	0.02	0.03	0.04	0.05	0.03	0.12	0.2	0.22	0.26	0.27	0.05	0.07	-0.14	0.17
ENN 1000m	0.23	0.04	0.05	0.04	1	0.61	0.47	0.38	0.26	0.44	-0.5	0.34	-0.5	0.46	0.44	-0.17	0.44	0.32	0.28	0.26	-0.19	0.17	0.34	0.3	0.28
ENN 1500m	0.25	0.09	0.02	0.05	0.61	1	0.85	0.75	0.64	0.43	-0.6	0.56	-0.72	-0.7	0.67	0.22	0.49	0.46	0.43	0.38	0.28	0.24	0.45	0.46	0.43
ENN 2000m	-0.14	0.11	0.09	0.07	0.47	0.85	1	0.92	0.86	0.35	0.59	0.67	0.85	0.84	0.82	0.29	0.54	0.59	0.59	0.55	0.46	0.31	0.51	0.56	0.54
ENN 2500m	-0.13	0.09	-0.2	0	0.38	0.75	0.92	1	0.95	-0.27	-0.51	0.62	0.83	0.87	0.89	0.23	0.47	0.54	0.58	0.56	-0.5	0.26	0.44	0.5	0.51
ENN 3000m	0.01	0.06	-0.2	0.02	0.26	0.64	0.86	0.95	1	-0.17	0.46	-0.61	0.78	0.83	0.87	0.25	0.45	0.53	0.57	0.59	0.57	0.28	0.43	0.49	0.5
WED ^b 500m	0.28	0.06	-0.21	-0.27	0.44	0.43	0.35	-0.27	-0.17	1	0.46	0.32	0.46	0.39	0.33	0.51	0.32	0.15	0.07	0.02	0.07	0.54	-0.4	0.25	0.19

WED 1000m	0	0.16	- 0.03	-0.17	-0.5	-0.6	- 0.59	-0.51	- 0.46	0.46	1	0.89	0.73	0.68	0.65	0.44	0.72	0.6	0.49	0.41	0.33	- 0.38	- 0.62	- 0.55	0. 46
WED 1500m	-0.1	0.2	0.07	- 0.02	- 0.34	- 0.56	- 0.67	- 0.62	-0.61	0.32	0.89	1	0.82	0.77	0.75	0.47	0.72	0.74	0.69	0.62	0.53	- 0.43	- 0.62	- 0.63	0. 58
WED 2000 m	0.05	0	0.16	- 0.03	-0.5	-0.72	- 0.85	- 0.83	- 0.78	0.46	0.73	0.82	1	0.98	0.94	0.39	0.61	0.62	0.63	0.58	0.48	-0.4	- 0.57	-0.6	0. 59
WED 2500m	0.02	0	0.19	- 0.04	- 0.46	-0.7	- 0.84	- 0.87	- 0.83	0.39	0.68	0.77	0.98	1	0.99	0.39	0.62	0.64	0.65	0.63	0.55	-0.4	- 0.58	- 0.62	0. 61
WED 3000 m	0.01	- 0.02	0.2	- 0.05	- 0.44	- 0.67	- 0.82	- 0.89	- 0.87	0.33	0.65	0.75	0.94	0.99	1	0.37	0.6	0.63	0.64	0.64	0.58	- 0.37	- 0.55	- 0.58	0. 58
Habitat div. ^c 500m	- 0.05	0.23	-0.19	0.03	-0.17	- 0.22	- 0.29	- 0.23	- 0.25	0.51	0.44	0.47	0.39	0.39	0.37	1	0.72	0.57	0.48	0.45	0.42	- 0.87	- 0.76	- 0.63	0. 55
Habitat div. 1000m	-0.12	0.2	0.02	0.12	- 0.44	- 0.49	- 0.54	- 0.47	- 0.45	0.32	0.72	0.72	0.61	0.62	0.6	0.72	1	0.89	0.77	0.71	0.65	- 0.66	- 0.89	-0.81	0.7 1
Habitat div. 1500m	-0.2	0.21	0.12	0.2	- 0.32	- 0.46	- 0.59	- 0.54	- 0.53	0.15	0.6	0.74	0.62	0.64	0.63	0.57	0.89	1	0.93	0.86	0.79	- 0.55	- 0.78	- 0.85	0. 8
Habitat div. 2000 m	-0.19	0.27	0.16	0.22	- 0.28	- 0.43	- 0.59	- 0.58	- 0.57	0.07	0.49	0.69	0.63	0.65	0.64	0.48	0.77	0.93	1	0.96	0.88	- 0.48	- 0.68	- 0.78	0. 82
Habitat div 2500m	- 0.22	0.26	0.13	0.26	- 0.26	- 0.38	- 0.55	- 0.56	- 0.59	0.02	0.41	0.62	0.58	0.63	0.64	0.45	0.71	0.86	0.96	1	0.97	- 0.46	- 0.62	-0.72	0.7 8
Habitat div 3000 m	- 0.25	0.23	0.08	0.27	-0.19	- 0.28	- 0.46	-0.5	- 0.57	- 0.07	0.33	0.53	0.48	0.55	0.58	0.42	0.65	0.79	0.88	0.97	1	-0.4	- 0.54	- 0.64	0.7 1
% arable 500m	0	- 0.23	0.03	- 0.05	0.17	0.24	0.31	0.26	0.28	- 0.54	- 0.38	- 0.43	-0.4	-0.4	0.37	0.87	0.66	0.55	0.48	0.46	-0.4	1	0.82	0.65	0. 55

% arable 1000m	0.08	-0.31	-	-	0.34	0.45	0.51	0.44	0.43	-0.4	-	-	-	-	-	-	-	-	-	-	-	0.54	0.82	1	0.91	0.81
% arable 1500m	0.13	-	-	-0.14	0.3	0.46	0.56	0.5	0.49	-	-	-	-	-	-	-	-0.81	0.85	0.78	-0.72	-	0.64	0.65	0.91	1	0.96
% arable 2000 m	0.11	-	-	-0.17	0.28	0.43	0.54	0.51	0.5	-0.19	-	-	-	-	-	-	-0.71	-0.8	0.82	0.78	-0.71	0.56	0.81	0.96	1	
% arable 2500m	0.12	-	-	-0.16	0.26	0.39	0.49	0.49	0.51	-0.13	-	-	-	-	-	-	0.65	0.75	-0.8	-0.81	-	0.53	0.75	0.9	0.98	
% arable 3000 m	0.15	-	-	-0.16	0.21	0.33	0.43	0.45	0.5	-	-	-	-	-	-	-	-	-	0.78	-0.81	-	0.47	0.68	0.84	0.93	
Distanc e from buildin gs (m)	0.09	0.01	-	-	-0.14	-0.12	-0.1	-	0.02	0.39	0.04	0.07	0.12	0.07	0.05	0	-0.11	0.09	0.09	-0.1	-0.17	0.01	0.08	0.06	0.02	

^aENN = mean Euclidean Nearest Neighbour for woodland; ^bWED = woodland edge density, ^cHabitat div = habitat diversity

Table S.4.5. Observed and expected number of Pipistrelle passes on arable farms

Arable farms					
		<i>P. pipistrellus</i>		<i>P.pygmaeus</i>	
Habitat	Relative habitat	Observed	Expected	Observed	Expected
Grass	0.07	15.5	18.3	19.5	18.2
Woodland	0.14	40.0	35.7	42.6	35.3
Built	0.06	30.0	15.3	17.8	15.2
Arable	0.72	165.5	181.8	168.6	179.9
Water	<0.01	0.0	1.1	2.5	1.1
Total	1.00	252	252	251	251
Mixed farms					
		<i>P. pipistrellus</i>		<i>P.pygmaeus</i>	
Habitat	Relative habitat	Observed	Expected	Observed	Expected
Grass	0.23	78.6	53.0	54.5	53.3
Woodland	0.21	46.8	49.3	92.3	49.5
Built	0.07	32.2	16.1	6.6	16.1
Arable	0.49	70.7	115.3	54.0	115.8
Water	<0.01	5.5	1.5	27.3	1.5
Total	1.00	234	234	235	235

Significant differences in observed and expected values are highlighted in bold.

Table S.4.6: Full SEM results for bats including correlated errors

Response	Predictor	Estimate	Std. Error	DF	Crit. Value	P value	Std. Estimate
<i>P. pygmaeus</i> Summer							
Bat activity	Tree height	0.056	0.02	64.32	7.711	0.007	0.33
Bat activity	WED 500m	0.015	0.006	61.49	5.733	0.02	0.285
Bat activity	habitat diversity 3000m	-1.68	1.037	21.05	2.52	0.127	-0.2
Bat activity	distance from water	>0.0001	0.000 7	64.97	0.159	0.692	-0.05
Bat activity	temperature	0.078	0.055	23.97	1.929	0.178	0.168
Bat activity	Farm type	0.294	0.174	20.32	2.789	0.11	0.203
Tree height	Farm type	-2.09	1.092	22.72	3.617	0.07	-0.25
WED 500m	Farm type	5.217	4.092	23.4	1.619	0.216	0.191
habitat diversity 3000m	Farm type	0.037	0.03	24.04	1.503	0.232	0.222
habitat diversity 3000m	WED 500m	>0.0001	0.000 4	53.14	0.798	0.376	0.058
~~WED 500m	~~Tree height	0.281	-	72	2.436	0.009	0.281
~~WED 500m	~~distance from water	-0.27	-	72	-2.36	0.011	-0.27
~~distance from water	~~habitat diversity 3000m	0.284	-	72	2.456	0.008	0.284
<i>P. pipistrellus</i> activity Summer							
Bat activity	Tree height	0.066	0.019	59.71	11.63	0.001	0.359
Bat activity	WED 1500m	-0.004	0.012	35.66	0.113	0.739	-0.05
Bat activity	Dist nearest building	-0.003	0.001	58.57	7.399	0.009	-0.27
Bat activity	Farm type	0.421	0.482	22.23	0.754	0.395	0.134
Bat activity	Proportion arable 3000m	1.259	1.724	24.94	0.519	0.478	0.118
Bat activity	temperature	-0.11	0.072	23.12	2.398	0.135	-0.22
Tree height	Farm type	-4.17	2.185	22.72	3.617	0.07	-0.25
WED 1500m	Farm type	15.62	7.045	23.97	4.913	0.036	0.386

Proportion arable 3000m ~~WED 1500m	Farm type	-0.03	0.057	24	0.243	0.627	-0.1
	~~Proportion arable 3000m	-0.57	-	72	-5.69	0	-0.57

P. pygmaeus activity Autumn

Bat activity	Tree height	0.118	0.039	67.82	8.614	0.005	0.34
Bat activity	ENN 1000m	-0.01	0.008	67.93	1.618	0.208	-0.16
Bat activity	Prop Proportion arable 3000m	1.864	2.536	19.72	0.529	0.476	0.085
Bat activity	distance from water	-0.002	0.002	66.96	1.035	0.313	-0.12
Bat activity	temperature	0.21	0.181	22.37	1.331	0.261	0.136
Bat activity	Farm type	0.576	0.348	21.61	2.687	0.116	0.195
Tree height	Farm type	-1.34	1.062	22.82	1.593	0.22	-0.16
ENN 1000m	Farm type	-9.38	5.329	22.81	3.081	0.093	-0.22
Prop							
Proportion arable 3000m	Farm type	-0.03	0.026	24	1.205	0.283	-0.21
~~ENN 1000m	~~Tree height	-0.27	-	75	-2.39	0.01	-0.27
~~ENN 1000m	~~distance from water	0.286	-	75	2.532	0.007	0.286
~~Prop							
Proportion arable 3000m	~~distance from water	-0.26	-	75	-2.27	0.013	-0.26

P. pipistrellus autumn

Bat activity	Tree height	0.098	0.034	52.52	8.151	0.006	0.223
Bat activity	WED 2500m	-0.06	0.041	31.95	1.757	0.195	-0.28
Bat activity	habitat diversity						
Bat activity	2000m	7.272	3.694	47.3	3.629	0.063	0.316
Bat activity	distance from buildings	-0.01	0.002	61.27	7.099	0.01	-0.22
Bat activity	temperature	0.764	0.326	24.52	5.39	0.029	0.394
Bat activity	Farm type	0.025	1.264	25.87	>0.00 01	0.985	0.003
Tree height	Farm type	-2.69	2.123	22.82	1.593	0.22	-0.16
WED 2500m	Farm type	14.52	6.649	24	4.768	0.039	0.39

habitat diversity 2000m	Farm type	0.136	0.055	23.97	6.046	0.022	0.421
~~mean temperature	~~WED 2500m	0.065	-	75	0.556	0.29	0.065
~~mean temperature	~~habitat diversity 2000m	0.07	-	75	0.598	0.276	0.07

Myotis spp Summer

Myotis presence	Tree height	0.063	0.035	72	1.803	0.071	0.254
Myotis presence	WED 1500m	0.04	0.016	72	2.426	0.015	0.382
Myotis presence	distance from water	-0.002	0.001	72	-1.37	0.172	-0.18
Myotis presence	Farm type	0.059	0.589	72	0.101	0.92	0.014
Myotis presence	habitat diversity 500m	0.473	1.337	72	0.353	0.724	0.056
Myotis presence	temperature	-0.06	0.091	72	-0.61	0.542	-0.08
Tree height	Farm type	-4.17	2.185	22.72	3.617	0.07	-0.25
WED 1500m	Farm type	15.62	7.045	23.97	4.913	0.036	0.386
habitat diversity 500m	Farm type	0.202	0.067	23.22	9.148	0.006	0.404
~~WED 1500m	~~habitat diversity 3000m	0.282	-	72	2.443	0.009	0.282

Myotis spp. autumn

Myotis presence	Tree height (scaled)	0.011	0.386	75	0.028	0.978	0.005
Myotis presence	ENN 1500m (scaled)	-0.87	0.637	75	-1.37	0.172	-0.37
Myotis presence	distance from water (scaled)	-0.53	0.401	75	-1.32	0.187	-0.23
Myotis presence	Farm type	-0.63	0.467	75	-1.34	0.18	-0.27
Myotis presence	habitat diversity 2500m (scaled)	0.509	0.512	75	0.994	0.32	0.217
Myotis presence	temperature (scaled)	0.391	0.456	75	0.858	0.391	0.167
Tree height (scaled)	Farm type	-0.16	0.124	22.82	1.593	0.22	-0.16

ENN 1500m (scaled)	Farm type	-0.33	0.179	23.98	3.311	0.081	-0.33
habitat diversity 2500m (scaled)	Farm type	0.275	0.169	24.71	2.628	0.118	0.276
habitat diversity 2500m (scaled)	distance from water (scaled)	0.12	0.043	50.01	7.93	0.007	0.12
habitat diversity 2500m (scaled)	ENN 1500m (scaled)	-0.27	0.094	68.41	7.604	0.008	-0.27

Table S.4.7: GLMM results for the effect of stocking rate and margin type on bat activity on mixed farms.

Summer					Autumn			
<i>P. pipistrellus</i>								
Distribution/ R ² value	Variable	Estimate	Std Error	P value	Distribution N. binomial/ R ² = 0.69	Estimate	Std Error	P value
Poisson/ R ² = 0.40	Tree height	0.53	0.15	0.0005		0.22	0.18	0.23
	Field type: 'grass-crop'	-0.34	0.27	0.201		-0.11	0.29	0.68
	Stocking rate cattle	-0.19	0.26	0.467		0.57	0.65	0.88
	Stocking rate cattle (poly 2)	-	-	-		-2.72	0.91	0.003
	Stocking rate cattle (ploy 3)	-	-	-		1.2	0.47	0.012
	Sheep presence	-0.08	0.55	0.891		0.49	0.60	0.869
<i>Myotis spp.</i>								
Binomial/ R ² = 0.26	Tree height	0.26	0.15	0.029	Binomial/ R ² = 0.40	0.78	0.44	0.076
	Stocking rate cattle	0.04	0.28	0.091		-0.31	0.66	0.634
	Field type: 'grass-crop'	-0.34	0.26	0.303		-0.19	0.80	0.809
	Sheep presence	0.49	0.60	0.869		-0.16	1.18	0.895
<i>P. pygmaeus</i>								
Poisson/ R ² = 0.38	Tree height	0.26	0.15	0.09	N. binomial/ R ² = 0.66	0.25	0.19	0.185
	Field type: 'grass-crop'	-0.34	0.26	0.20		-0.22	0.33	0.502
	Sheep presence	0.49	0.59	0.41		1.74	0.49	0.0004
	Stocking rate cattle	0.04	0.28	0.89		0.74	0.25	0.003

Note: R2 values reported are conditional r2.

2.4. Chapter 5: Impacts of regenerative agriculture on biodiversity: does ‘mob-grazing’ benefit moths?

Abstract

Lepidoptera are a highly diverse order of insects, providing essential pollination services and food for higher taxonomic groups. However, the populations of many common and widespread species of moth are in decline. High livestock stocking rates associated with intensive farming are known to be detrimental to moth communities. ‘Mob grazing’, a type of rotational grazing that is gaining popularity in the UK and the United States, aims to mimic the grazing behaviour of wild megaherbivores by increasing herd numbers but also pasture rest periods. Anecdotal evidence suggests that this practice could be beneficial for biodiversity, but scientific evidence to support this is limited. I investigate whether mob grazing cattle is beneficial for moths in comparison to more widespread ‘set-stock’ grazing systems. I measured abundance and species richness of moths in thirteen mob grazed fields and thirteen set-stock fields across Scotland (United Kingdom). I did not detect any direct effect of mob grazing on moths in either larval or adult forms. However, mob grazing mitigated the negative effect of sheep grazing on caterpillar abundance and species richness, likely by reducing overall grazing pressure through longer pasture rest periods. Caterpillar abundance and species richness was lower in fields grazed at a higher grazing intensity. Pasture composition was also important, with lower caterpillar abundance associated with high cover of ryegrass (*Lolium* spp.), a grass species that is indicative of more intensively managed pastures. To my knowledge, this is the first time that the effects of mob grazing on moths have been explored. These findings can inform agricultural policy that financially support regenerative farming practices.

5.1. Introduction

In grassland ecosystems, large grazers, or 'megaherbivores' play a key role in sustaining biodiversity. Grazing limits the growth of competitive plant species, allowing more light and nutrient resources for less competitive species. At certain stocking levels, grazers can increase plant diversity (Kapás et al., 2020; Pakeman et al., 2019) with potential bottom-up benefits for taxa at higher trophic levels. Most large grazers also browse plants selectively, creating a variety of vegetation heights and micro habitats (Schmitz and Isselstein, 2020) which can in turn increase insect diversity (Jerrentrup et al., 2014). In addition, megaherbivores provide much needed nutrients to plants through defecation and may even increase plant diversity through seed transport (Cosyns et al., 2005). In a 'natural' ecosystem these large grazers stay together in thousands, or historically, millions of individuals as was seen in North American bison *Bison bison* (Shaw, 1995) Because of the presence of predators these megaherbivores would stay close together and be constantly on the move. This grazing behaviour results in grasslands that are put under extreme grazing pressure and trampling by large herds, but only for a very short period of time, as herds will likely not return to that area for months or even years, allowing pasture to recover.

These natural grassland systems are very different to the way that I manage domestic livestock today. In Europe, the majority of cattle and sheep are managed as 'set-stocked' systems, where animals are kept in much lower herd numbers than usually seen in the wild and are grazed in the same field for the entirety of the grazing season, or at least for several weeks. In the United Kingdom (UK), cattle population density is highly variable, ranging from 0.1 to 1.86 cattle per hectare of pasture (Matthews, 2023).

Continuous grazing pressure can lead to over-grazing, where vegetation is grazed to a point where recovery takes longer or does not occur at all, areas of bare ground increase and soil becomes compacted (da Silva et al., 2019). In

fact, high stocking densities generally have a negative impact on a variety of insect taxa, reducing abundance or biomass of foliar arthropods, grasshoppers, bees, wasps and their parasitoids (Dennis et al., 1998; Kruess and Tscharntke, 2002).

'Mob grazing', a type of rotational grazing has been proposed as a potential solution to this apparent trade-off between food production and maintaining biodiversity. Also called 'adaptive multi-paddock (AMP) grazing', 'regenerative grazing', 'high density short duration' (HDSD), or 'tall grass grazing', mob grazing has seen a surge in popularity in the United States of America (USA; Gordon, 2010; Thomas, 2012) and is now gaining momentum in the UK. The UK Agricultural and Horticultural development Board (AHDB) defines mob grazing as 'Grazing with a high density of stock for a short duration, coupled with a long rest period' (AHDB, n.d.). This grazing strategy is designed to mimic wild megaherbivore behaviour by keeping animals in a large herd and constantly on the move.

One of the major reasons why some farmers have adopted mob grazing in the UK is to improve soil health (Wagner et al., 2023). Indeed, numerous studies have shown that mob grazing can increase soil organic carbon, soil nitrogen and/or water filtration (Apfelbaum et al., 2022; Johnson et al., 2022; Mosier et al., 2021; Teutscherová et al., 2021), making this an attractive strategy for farmers to increase pasture productivity and reduce the need for fertiliser inputs. These positive effects of mob grazing on soil health seem to extend to below-ground invertebrates. Mob grazing increased earthworm abundance in comparison to traditional grazing in a tropical grazing systems (Teutscherová et al., 2021). In addition, livestock farmers in the UK practising mob grazing have reported faster pasture recover times and an increase in above-ground biodiversity, such as increasing numbers of small mammals and hunting birds (Wagner et al., 2023). Agricultural online resources report anecdotal observations on the benefits of mob grazing for biodiversity (Willis, 2020), however, scientific evidence of the benefits of mob grazing for pasture plant

diversity is limited and sometimes contradictory. Grenke et al., (2022) found that there were no differences in plant community composition or species evenness between mob-grazed fields and traditional local grazing, but that plant species richness was lower in mob-grazed fields, with a trend for fewer native species in this treatment. Conversely, plant diversity was higher and species richness of non-native plants was lower in mob-grazed fields than in set-stock fields in other studies (Hillenbrand et al., 2019; Schmid et al., 2024b). There is also relatively little research so far on the impacts of mob grazing on above-ground invertebrates and it is limited to the USA, where mob grazing can increase dung beetle species richness (Wagner et al., 2021), foliar arthropod species richness (Schmid et al., 2024) and overall invertebrate biomass in adjacent streams (Saunders and Fausch, 2007). Understanding the conditions under which mob grazing might enhance biodiversity requires research across a variety of taxa and a greater climatic range.

Lepidoptera are good ecological indicators of grassland habitat quality (Collinge et al., 2003; Erhardt, 1985; Rákossy and Schmitt, 2011) and are a well-studied taxa in Europe (Waring and Townsend, 2018). As adults, moths are important pollinators of wildflowers (Walton et al., 2020) and both larvae and adults are a valuable food source for taxa at higher trophic levels (Aldasoro et al., 2019; Vickery et al., 2001). Many species of moths feed on grasses or forbs in their larval form and are likely to be impacted by grazing management practices. In fact, Lepidopteran caterpillars have been found to respond negatively to year-round grazing of sheep compared with summer grazing only (Cole et al., 2010), with high cattle stocking rates also decreasing caterpillar species richness and abundance in comparison to ungrazed or extensively grazed pastures (Kruess and Tschardt, 2002). The survival rates of the caterpillars of a rare butterfly species, *Phengaris alcon*, decreased rapidly with even low levels of cattle grazing (Moschetti et al., 2020) as did the survival of *Euphydryas aurinia* larvae in grazed versus ungrazed plots (Johansson et al., 2024). Similarly, high intensity sheep grazing reduced nest survival of a

hibernating caterpillar in comparison to low intensity and ungrazed fields, *Melitaea cinxia* (van Noordwijk et al., 2012). However, for *Ocnogyna loewii* larvae, cattle grazing seems to be beneficial at both moderate and high stocking rates (0.55 cows ha⁻¹, 1.1 cows ha⁻¹) by reducing vegetation height thus creating warmer microclimates (Berman et al., 2018). Adult moths have also been found to respond to grazing management in a number of studies, with species richness often declining with increasing grazing intensity (Dumont et al., 2009; Kruess and Tschardt, 2002; Littlewood, 2008; Pöyry et al., 2004). To my knowledge, the impacts of mob grazing on Lepidoptera have not yet been explored.

This study investigates the effects of mob grazing compared to set-stocking in Scotland (UK) on both Lepidoptera larvae and adults.

Specifically, I address the questions:

Does mob grazing cattle increase the abundance, species richness and diversity of Lepidoptera in either larval or adult form in comparison to set-stocked grazing? (Q1)

I also assess the influence of other attributes of grazing management (livestock grazing intensity, presence of sheep and sward composition) likely to interact with mob grazing (Q2).

5.2. Methods

5.2.1. Site selection

This study took place in Scotland between latitudes of 55.3°N and 57.4°N (Fig.1). The climate is cool wet oceanic, though rainfall can vary across the country between 150 and 250 days of rainfall per year. Almost 50% of land in Scotland is grazed by domestic livestock, with pastures varying from

agriculturally improved pastures to semi-natural grassland. Altitude of sites selected for this study ranged between 11 m to 347 m above sea level (mean = 176 m).

In the UK, mob grazing is mostly used for managing cattle herds rather than sheep (Wagner et al., 2023), so I focussed my study on cattle. The definition of mob grazing is variable and open to interpretation, with large variation on how it is implemented from one farm to another (Bork et al., 2021; Wagner et al., 2023). Therefore, rather than limiting farms to certain criteria, I considered all farms that were claiming to manage cattle by mob grazing for at least one full year prior to data collection. I collected information on livestock management practices associated with mob grazing: stocking rate, paddock size and pasture rest period. Stocking rate for each field was measured in livestock units (LUs) per hectare, with one LU approximately equivalent to one suckler cow and calf (UK Government, 2021), followed by the number of days that livestock were kept in the paddock, enabling a calculation of grazing intensity ($\text{LUs Ha}^{-1} \text{yr}^{-1}$). Farms were recruited using social media advertising, contacting farmers with publicly available contact details or by recommendations made by contacts from agricultural organisations. Thirteen mob grazed fields were selected across Scotland (Figure 5.1). These were each then paired with a nearby set-stock field. In some cases, the two treatment types were practiced on the same farm. Otherwise, mob grazing farms were asked to recommend a neighbouring farmer who managed cattle in a set-stock system. Mean distance between fields of the same pair was 3.6 km (min = 0.1 km, max = 16 km). When pairs were not on the same farm, I ensured that soil type was the same within pairs of fields with the use of soil maps (Soil Survey of Scotland Staff, 1981). Soil types were mostly cambisols (young soil), podzols (clayey) or stagnosols (very wet soil). Three out of the 13 mob-grazed fields were also certified organic. One of these was paired with an organically managed set-stocked field on the same farm, one was paired with a set-stocked field on a nature reserve with no synthetic inputs, whilst the other was paired with a set-stocked field on a farm

that was being managed using principles of regenerative agriculture (reduced inputs and no-till) but was not yet certified organic. Ten out of 26 fields also had sheep grazed on them over the winter months (managed as a set-stocked system), four of these were mob-grazed fields whilst six were set-stocked.

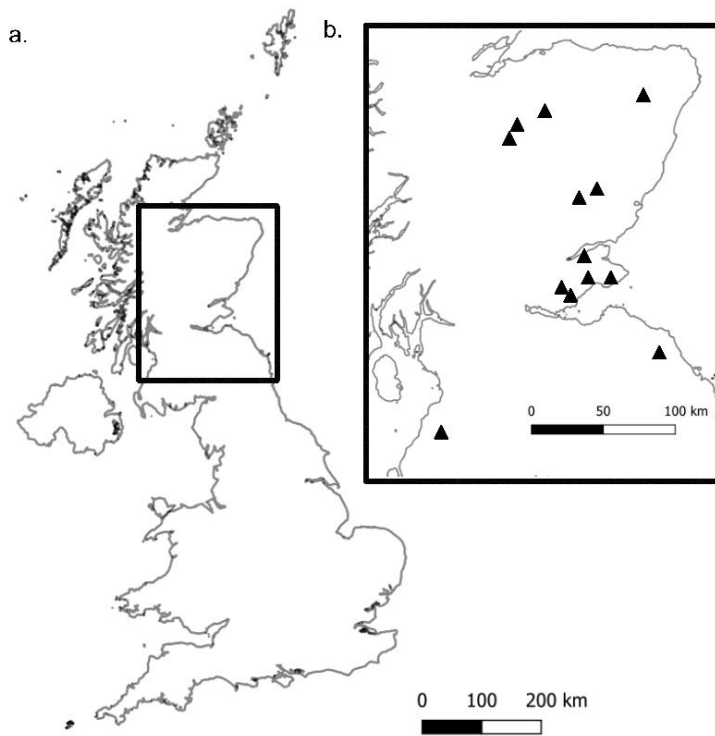


Figure 5.1. Map showing location of the study area within the UK (a) and approximate location of farm pairs (b), indicated with a triangle. Map created using Ordnance Survey base map (Edina, 2024).

5.2.2. Surveying moth larvae

Caterpillar sampling was carried out between 18th March and 10th June 2023. During this period a large number of grass-feeding moths are in their larval stage (Cook et al., 2022) and many are nearing final instar stages which facilitates identification to species level. All caterpillar surveys were carried out at least one hour after sunset during dry weather (Boyes et al., 2021). Minimum temperature at sunset was 5°C and maximum windspeed was three on the Beaufort scale. I used two methods to survey for caterpillars, sweep-netting along transects (Boyes et al., 2021) and timed manual searches within quadrats.

Though I were not always able to carry out both methods, the approach used was consistent across each field pair (transect survey nights $n = 18$, quadrats $n = 4$, both $n = 20$) and each pair was sampled on the same night. The order in which fields were sampled (i.e. mob or set-stocked first) was alternated each night. I sampled as many sites as possible twice, resulting in eight out of 13 pairs being sampled on two separate occasions, with the rest being sampled once.

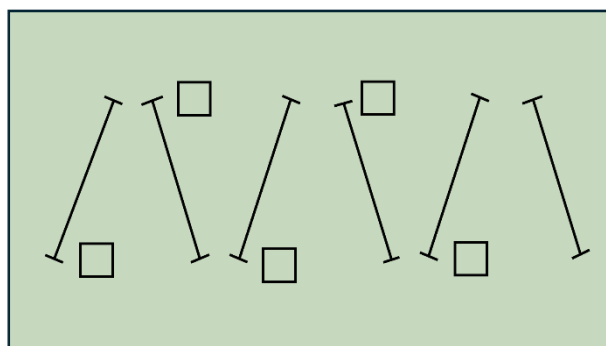
5.2.3. Sweep netting

Many species of grass-feeding caterpillar hide underground or in leaf litter during the day but will ascend vegetation after dark to feed (Sterling and Henwood, 2020), making sweep-netting an effective method for collecting caterpillars feeding at the tops of vegetation in grassland (Boyes et al., 2021). Six transects per field were walked on diagonal lines across the field (Figure 5.2.) and at a steady pace using a sweep net with a 50 cm diameter, pentagon-shaped frame (NHBS, 2023). Each transect consisted of 15 sweeps with one step taken between each sweep. The net was checked for caterpillars and emptied at the end of each transect. The same surveyor carried out transect sampling across all fields for consistency of technique. Following sweep-netting, three random measurements of vegetation height were taken along the transect by a second surveyor using a drop disc (25 cm diameter, 46 g).

5.2.4. Manual searches

In some cases, vegetation height was too low for sweep-netting, so manual searches were conducted. Five 1 x 1 m quadrats were placed adjacent to transect start points to avoid disturbance (Figure 5.2) and searched by one

surveyor passing a torch over the vegetation for a period of three minutes. When a larvae was found, the timer was stopped to enable the individual to be



— : transect location

□ : quadrat location

potted and re-started when the surveyor was able to continue the search.

Figure 5.2: Survey design of transects and quadrats within a field.

5.2.5. Species identification

Species identification was carried out using Sterling and Henwood (2020). Individuals that could be confidently identified in the field were then released into suitable habitat, whilst those that were harder to identify or that were too small to accurately identify at the time of sampling were kept in rearing pots until either they reached final instar or pupated and emerged as adults, (after which they were then also released). I was only able to identify some individuals to genus (usually one of two species that were functionally similar) and these were thus into one 'species group' for analysis (Table S.5.1.).

5.2.6. Surveying adult moths

Between 12th July 23rd August 2023 adult moths were surveyed using UV LED light traps based on the light trap design in Infusino et al., (2017) with a solar sensor that activated traps at dusk and deactivated them at dawn. Minimum sunset temperature for moth trapping was 11°C and wind speed never

exceeded three on the Beaufort scale. To reduce attraction of moths from nearby hedgerows or woodlands, each trap was placed in the middle of each field, at least 50 m from the field edge (Merckx et al., 2009). Each pair of mob-grazed and set-stocked fields was surveyed on the same night, with a total of eleven pairs being surveyed (I was unable to survey two fields pairs due to the presence of cattle in the field). Traps were emptied shortly after dawn and moths were identified in the field, aided where necessary by Waring and Townsend (2018) for macro moths (larger moths) and Sterling and Parsons (2018) for micro moths (smaller moths). Each moth species was also assigned a broad food-plant category (or guild) using the same identification guides. Categories assigned were grasses, forbs, mosses, lichens, woody plants and decaying plant material, with an additional 'broad' guild for species feeding on more than one plant category (Table S.5.2.).

5.2.7. Plant surveys

To examine the potential effects of pasture composition on moths, plant surveys were carried out during the summer months (at the same period as adult moth surveys) to identify grasses and flowering forbs. Quadrats measuring 2 x 2 m were randomly placed in ten different locations in each field. Percentage cover of each vascular plant species present within the quadrat was recorded, with all mosses grouped into one category: 'moss'. Some grasses were identified to genus level such as ryegrasses (*Lolium* spp.), meadow grasses (*Poa* spp.) and fescues (*Festuca* spp.). I also calculated plant diversity index (Shanon-Weiner) and total species richness for each field.

5.2.8. Data analysis

All data analysis was carried out in R version 4.3.2 (R Core Team, 2023b). To assess the effect of grazing management type, pasture characteristics and grazing intensity on moths (Q1 +Q2), I built generalised mixed effect models (GLMMs). Separate GLMMs were run for caterpillar abundance, caterpillar species richness, adult moth abundance, adult moth species richness, and adult moth diversity (Shannon index). The number of caterpillar species was low (mean = 1.7, min = 0, max = 7) so I did not consider a diversity metric for this group.

For caterpillar GLMMs data from transects and quadrats was combined to obtain one value per visit, 'farm' nested within 'pair' was included as a random effect to account for differences in sampling method and multiple visits per farm. Caterpillar abundance and species richness were modelled using a Poisson distribution and glmmTMB package was used to aid with model convergence (Brooks et al., 2017). Adult moths were only surveyed once on each farm so no random effect was necessary. All adult moth count data was modelled in lme4 (Douglas Bates et al., 2015) using a Poisson distribution unless overdispersion was detected, in which case I used a negative binomial distribution and the MASS package (Venables and Ripely, 2002). Adult moth diversity was modelled using lme4 and a gaussian distribution.

Each model included grazing management type (either set-stocked or mob-grazed), grazing intensity and the presence of sheep as fixed effects. I excluded stocking rate, pasture rest period and vegetation height as these were significantly associated with grazing management (Figure. S.5.1). Ryegrass (*Lolium perenne*) is often associated with intensively managed pasture and higher fertiliser inputs (Jakusek et al., 2020; Kruess and Tscharntke, 2002; Labuschagne and Agenbag, 2006). Pastures with higher plant species richness and diversity may affect caterpillar or moth abundance/ species richness by providing a variety of food plant or nectar resources (Tyler, 2020). To avoid

over-saturating GLMMs I selected one pasture vegetation characteristic (percentage ryegrass cover, plant diversity or plant species richness) to include as a fixed effect for each model (whichever gave the highest r^2 value based on preliminary analysis; Table S.5.4). Finally, to assess if the effects of mob grazing cattle change in with the presence of sheep grazing and pasture composition (Q2), two interaction terms were included: grazing management type x sheep presence and grazing management type x vegetation characteristics.

I then selected the most parsimonious models by calculating Akaike's information criterion (AICc, corrected for small sample size) for all possible combinations of variables using the MuMIn package (Burnham and Anderson, 2004). Model averaging was conducted (using equal weighting) across all models that were within $AICc = 2$ (ΔAIC) of the most parsimonious model (Arnold, 2010). I refer to all models with $\Delta AIC < 2$ as 'final models'. All final models were checked for goodness of fit using the DHARMA package (Hartig, 2024). Alternative models and associated AICc values are given in Table S.5.5.

5.3. Results

5.3.1. Overview

I recorded a total of 218 individual caterpillars of 18 species across 13 pairs of fields. All species were macro moths except two species of butterfly (which were also included in analyses). Mean caterpillar abundance in set-stock fields per visit was 4.3 whilst mean abundance in mob-grazed fields was 4.8. Mean species richness per visit was overall low, but was higher in mob-grazed fields (mean = 2.1) than in set-stock fields (mean = 1.2). All species found in larval form were grass or forb-feeding species, aside from one individual.

Moth trapping for adult Lepidoptera yielded 434 individual moths of 60 species across 11 pairs of fields. Micro moths made up 21% of total moth

abundance. Total moth abundance was almost identical between grazing treatments, with 216 individuals in mob grazed fields and 218 individuals in set-stock fields. I identified 41 species across all mob-grazed fields and 38 species across all set-stock fields. Adult moths from the family Noctuidae made up 70% of the total catch from light traps. Around half of the moth species found were species that feed on woody plants in their larval form, though these only made up 22% of total moth abundance with the majority of moth abundance composed of grass or forb-feeding species (Table S.5.2.).

Cattle herds in mob-grazed fields were higher (mean = 53.9 LUs, min = 5 LUs, max = 140 LUs) than in set-stock stock fields (mean = 16.3 LUs, min = 1.3 LUs, max = 38.5 LUs), with smaller paddocks used in mob-grazed systems (mean = 2.1 Ha) than in set-stock systems (mean = 14.3 Ha). Mob-grazed fields were also given a significantly longer number of rest days across the year (mean mob = 357 days, mean set = 242 days, Figure S.5.1). However, grazing intensity was similar between set-stock and mob-grazed fields (Figure S.5.1).

5.3.2. Effects of livestock grazing management on Lepidoptera

I did not find a direct significant effect of mob-grazing on Lepidoptera. However, the interaction between grazing treatment and sheep grazing was marginally significant for caterpillar abundance and species richness (Table 5.1). The presence of sheep in set-stock systems marginally reducing mean caterpillar abundance by almost 40% and mean species richness by over 80% (Figure 5.3a,b). The presence of sheep alone (without interaction) also significantly reduced caterpillar abundance by over 30% and marginally reduced adult moth abundance and species richness by 2.7% and 2.3% respectively.

Grazing intensity had a significant negative effect on larval abundance and species richness (Figure 5.3c,d). An increase of $0.8 \text{ LUs Ha}^{-1} \text{ yr}^{-1}$ (e.g. one beef

cow without calf) was associated with a reduction of just over 20% in mean larval abundance and just under 40% in mean larval richness. Although grazing intensity was not significant, it was included in the top AIC models for adult moth abundance, and the direction of the response was negative (Figure 3e).

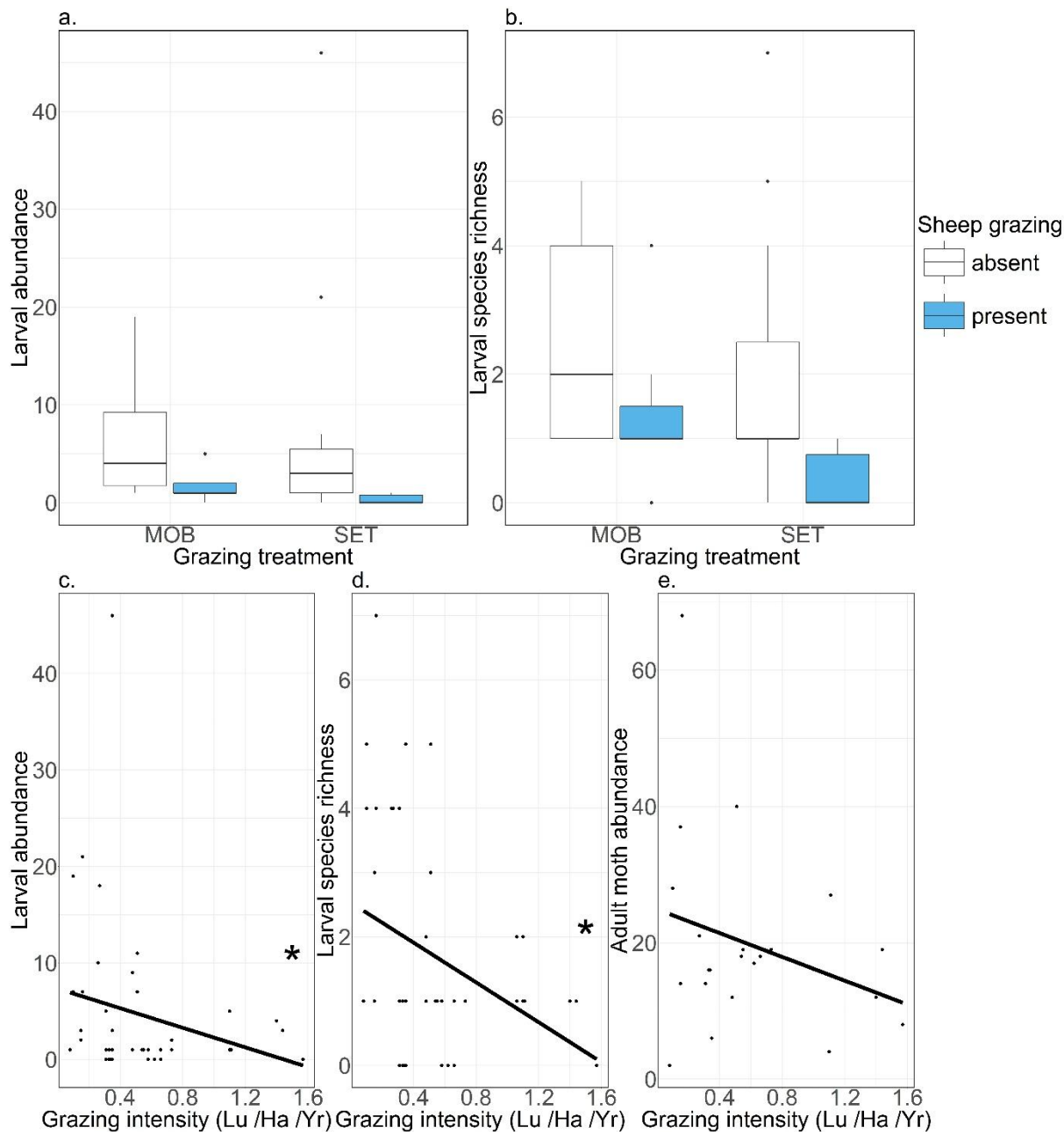


Figure 5.3. Boxplots showing the interaction between grazing treatment and the presence of sheep grazing on larval abundance (a.) and larval species richness (b.), and scatterplots showing the effect of grazing intensity on c. larval abundance, d. larval species richness and e. adult moth abundance. ****: $p \leq 0.001$, ***: $p \leq 0.01$, **: $p \leq 0.05$.

5.3.3. Effects of pasture composition

An increase in just under 30% ryegrass cover significantly reduced caterpillar species richness by 18%. This variable was also retained in the final models for adult moth abundance and species richness but had no significant effect, though the direction of effect was also negative (Table 5.1). Plant species richness was only included in the adult moth diversity but was not retained any of the final models ($AICc < 2$). A full list of all plant species recorded is available in Table S.5.3.

Table 5.1. Summaries for averaged models, using averaging across all models with $\Delta AICc < 2$

Predictor	Estimate	Adjusted SE	z value	Pr(> z)
<i>Caterpillar abundance</i>				
(Intercept)	1.34 (± 0.46)	0.47	2.86	0.004
Grazing intensity (LU Ha ⁻¹ yr ⁻¹)	-0.49 (± 0.19)	0.19	2.54	0.011
Treatment (set-stock)	-0.30 (± 0.49)	0.51	0.60	0.549
Sheep (present)	-1.47 (± 0.63)	0.65	2.26	0.024
Sheep (present) x Treatment (set-stock)	-1.81 (± 0.94)	0.98	1.85	0.064
<i>Caterpillar species richness</i>				
(Intercept)	0.69 (± 0.23)	0.24	2.87	0.004
Grazing intensity	-0.33 (± 0.17)	0.16	2.02	0.044
Sheep (present)	-0.62 (± 0.45)	0.46	1.36	0.172
Perc ryegrass	-0.31 (± 0.16)	0.16	2.02	0.043
Treatment (set-stock)	-0.18 (± 0.32)	0.33	0.54	0.586
Sheep (present) x Treatment (set-stock)	-1.39 (± 0.72)	0.75	1.85	0.064
<i>Adult moth abundance</i>				
(Intercept)	3.04 (± 0.16)	0.17	17.88	<0.0001
Perc ryegrass	-0.23 (± 0.14)	0.15	1.55	0.120
Sheep	-0.52 (± 0.29)	0.31	1.69	0.091
Grazing intensity	-0.22 (± 0.13)	0.14	1.52	0.127
<i>Adult moth species richness</i>				
(Intercept)	2.03 (± 0.10)	0.11	19.24	0.00
Sheep (present)	-0.17 (± 0.09)	0.10	1.76	0.08
Perc ryegrass	-0.29 (± 0.20)	0.21	1.42	0.16
<i>Adult moth diversity index</i>				
intercept	1.65 (± 0.14)	0.15	11.22	<0.0001
Sheep	-0.27 (± 0.27)	0.29	0.93	0.352

5.4. Discussion

In this study I investigated the effects of mob grazing on moth abundance, species richness and diversity, for the first time. Whilst there was no direct effect of grazing management (mob or set-stock grazing) on moths, mob grazing (marginally) reduced the negative effect of sheep grazing on caterpillar abundance and species richness. Grazing intensity of cattle significantly reduced larval abundance and species richness. Lower species richness of caterpillars was also associated with fields with a higher cover of ryegrass.

5.4.1. Mob grazing and livestock management

I found an interaction between grazing treatment (mob or set-stock grazing) and the presence of sheep grazing. The combination of set-stocking and sheep grazing marginally reduced both larval abundance and species richness in comparison to mob-grazed fields. In addition, pastures grazed by cattle only had significantly higher caterpillar abundance than those that those with combined cattle and sheep grazing, as well as marginally higher adult moth abundance and richness. Previous studies have shown that sheep grazing reduces Lepidoptera abundance and diversity compared to cattle grazing (Cutter et al., 2022; Öckinger et al., 2006), however there is a lack of research comparing cattle only with mixed cattle and sheep systems. What is interesting in my study is that mob grazing mitigates the effects of sheep grazing, with the management of cattle by set-stocking likely creating an additional pressure on Lepidoptera where fields are also grazed by sheep. The mob grazed fields in this study had significantly taller vegetation than set-stock fields and significantly greater number of pasture rest days per year (Figure S.5.1). Thus, when set-stocking is combined with the additional pressure of sheep grazing,

this likely further reduces vegetation height, leaving very little food for caterpillars. Indeed, taller vegetation could increase survival of larvae by providing more food resources (Kruess and Tscharntke, 2002) and can also increase egg-laying (Fartmann, 2006). Mob grazing farmers may also be more likely to adopt other regenerative farming practices that were not measured in this study. In fact, rotational grazing is thought to reduce the need for wormers due to regular moving of cattle reducing the likelihood of consuming parasite eggs from dung (Rapiya et al., 2019). Anthelmintics have negative effects on non-target invertebrates (Scheffczyk et al., 2016) and could, therefore, be detrimental to Lepidoptera. Although all participating farmers in this study used wormer on their cattle, I did not collect information on the frequency of worming or chemicals used. Further research into the potential for mob grazing to reduce the use of anthelmintics may help to clarify these mechanisms.

Higher caterpillar abundance and species richness was associated with lower levels of grazing intensity. Overall grazing intensity across the year did not differ between the mob-grazed and set-stock fields in my study, and stocking rates were typical of these systems in the UK (Wagner et al., 2023). However, it is important to highlight that mob grazing elsewhere (such as the USA) is often done with much larger herds (77 LUs ha^{-1} , (Tracy and Bauer, 2019)). Thus, the benefits of mob grazing found in this study apply to the stocking rates used by my study participants (mean = 63 LUs Ha^{-1}). In addition, I show the benefits of mob grazing in cool, wet climatic regions and caution the application of this grazing strategy in drier regions where mob grazing under drought conditions may exacerbate the effects of trampling on plant communities (Souther et al., 2020).

5.4.2. Pasture composition

I found that a higher percentage cover of ryegrass was associated with lower caterpillar abundance. Though little is known about specific grass species eaten by caterpillars, some are reported to feed on meadowgrasses (*Poa* spp.), cocksfoot (*Dactylis glomerata*), or fescues (*Festuca* spp.) (Henwood and Sterling, 2022). Anecdotal observations when raising caterpillars for identification purposes during this study was that ryegrass offered was rarely eaten, whereas meadowgrasses were popular for some species. Though larval feeding preferences may differ in captivity, it could be that ryegrass is less palatable than other grass species, with some laboratory experiments suggesting that Lepidoptera larvae may avoid *Lolium perenne* where certain fungal species are present as symbionts (Shiba and Sugawara, 2010; Vicari et al., 2002). Furthermore, ryegrass species require high nutrient inputs and is often dominant in pasture seed mixes. As such, this grass species is often associated with higher nitrogen fertiliser applications, regular re-seeding and lower plant diversity (Van Dobben et al., 2019). This makes ryegrass a good indicator of higher fertiliser inputs and more intensively managed pastures.

Plant composition had no significant effect on adult moths. In addition, r^2 values for all adult moth final models were much lower than for caterpillar models. This lack of effect is likely due to adult moths being far more mobile than in their larval form. Around half of the adult moth species found in my study were woody plant-feeding species, so likely to have travelled to the light trap from habitats outside of the pasture, highlighting the importance of larval sampling for testing the effects of field-scale management practices.

5.4.3. Management recommendations

To my knowledge, this study is the first to report on the effects of mob grazing for moths. Whilst I did not find a direct benefit of mob grazing for moths, this grazing strategy did mitigate the effects of sheep grazing on caterpillar abundance and species richness. I also found evidence of a negative effect of higher grazing intensity on both larval abundance and species richness, and a negative effect of sheep grazing for both larvae and adult moths. This research can be used to support decisions on future agricultural policies as governments push for a move towards regenerative farming, particularly since mob grazing currently is not supported by environmental subsidies. My findings also feed into the growing body of evidence that grazing at high livestock stocking rates is detrimental to biodiversity, and lower stocking rates should be favoured in future policies.

Acknowledgements

This project was part funded by SRUC and part funded by a Diarsia Award (in memory of Douglas Boyes) from Butterfly Conservation. I would like to thank all farmers and landowners for granting access to land, including Tentsmuir nature reserve. I would also like to thank SRUC students who provided valuable assistance with fieldwork: Vanesa Conjar, Trudi Hayes, Clare Stewart, Emma Hathaway and Heather Lawson with special thanks to Charlotte Wood. Thanks also extend to Dr Mark Young for providing valuable advice on how to successfully raise caterpillars in captivity.

Supplementary material for Chapter 5

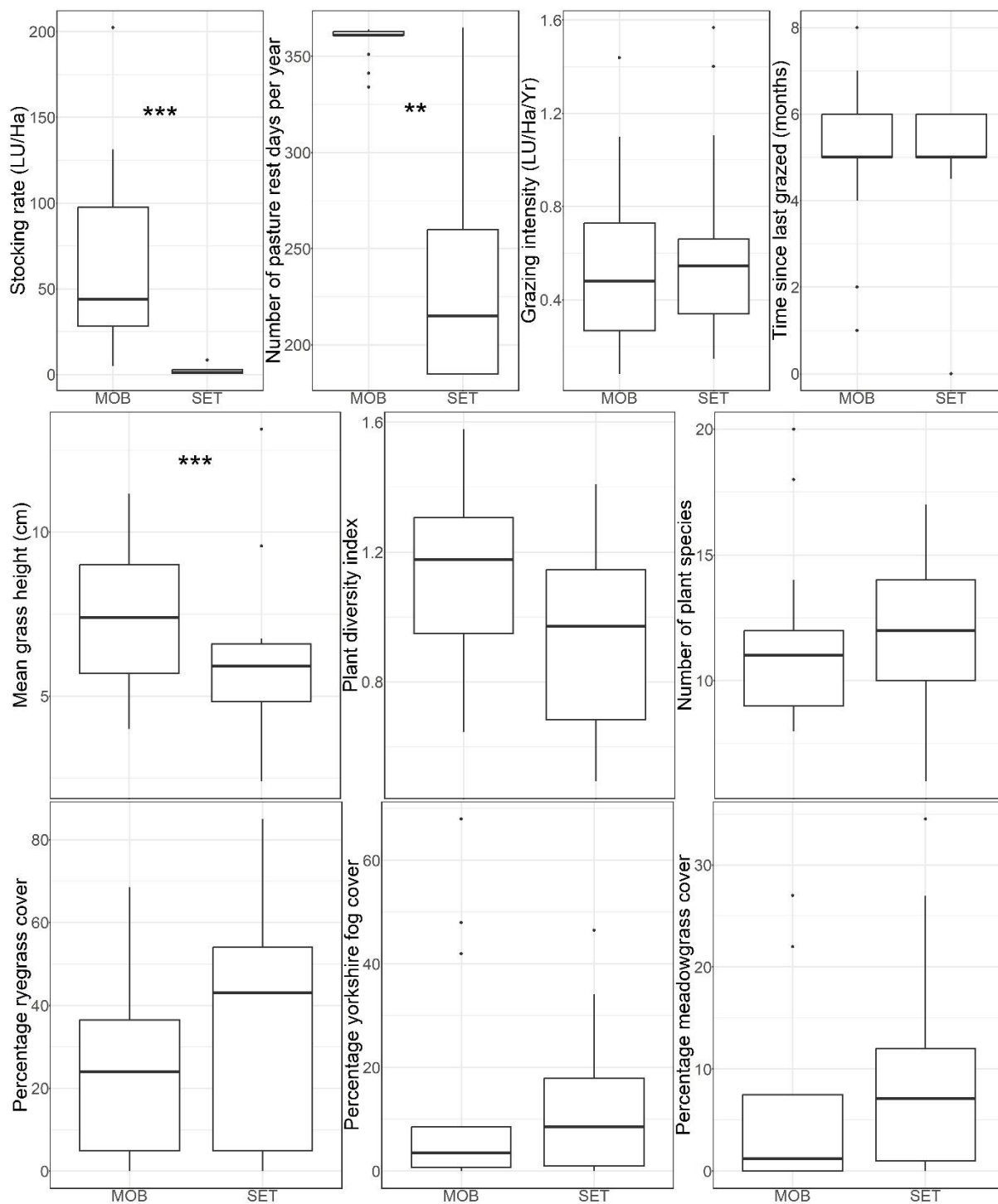


Figure S.5.1. Boxplots showing the differences between mob-grazed (MOB) and set-stocked (SET) for measures of vegetation characteristics and cattle stocking management. Significant differences were identified using Wilcoxon unpaired testing. Significance stars: '***' $\leq p = 0.001$, '**' $\leq p = 0.01$, '*' $\leq p = 0.05$.

Table S.5.2. Abundances of all species found during larval surveys (sweep-netting and manual searches combined) with detailed information on family, overwintering strategy and guild classification ('broad foodplant')

Species	Abundance in manual searches	Abundance in sweep netting	Family	Overwintering strategy	Broad foodplant
<i>Apamea crenata</i>	0	2	Noctuid	Larva	Grass
<i>Apamea monoglypha/lithoxylaea</i>	1	0	Noctuid	Larva	Grass
<i>Apamea remissa</i>	1	6	Noctuid	Larva	Grass
<i>Apamea remissa/crenata</i>	1	5	Noctuid	Larva	Grass
<i>Cerapteryx graminis</i>	0	44	Noctuid	Egg	Grass
<i>Eugnorisma glareosa</i>	1	0	Noctuid	Larva	Grass
<i>Agrochola litura</i>	0	6	Noctuid	Egg	Broad
<i>Mythimna ferrago</i>	0	2	Noctuid	Larva	Grass
<i>Mythimna spp.</i>	0	1	Noctuid	Larva	Grass
<i>Mesapamea secalis</i>	6	48	Noctuid	Larva	Grass
<i>Maniola jurtina</i>	1	6	Nymphalidae	Larva	Grass
<i>Alcis repandata</i>	1	0	Geometridae	Larva	Woody
<i>Amphipyra tragopoginis</i>	0	1	Noctuid	Egg	Broad
<i>Mythimna conigera</i>	0	1	Noctuid	Larva	Grass
<i>Mythimna impura</i>	2	18	Noctuid	Larva	Grass
<i>Noctua pronuba</i>	6	0	Noctuid	Larva	Grass
<i>Aphantopus hyperantus</i>	1	0	Nymphalidae	Larva	Grass
<i>Diarsia rubi</i>	3	6	Noctuid	Egg	Forbs
<i>Mesotype didymata</i>	0	2	Geometridae	Egg	Woody
<i>Mythimna impura/pallens</i>			Noctuid	Larva	Grass
<i>Xestia xanthographa/sextrigata</i>	6	10	Noctuid	Larva	Grass
<i>Xestia xanthographa</i>			Noctuid		Grass
Total	32	160			

Table S.5.3. Adult moth species recorded during light trapping.

Species	Total abundance	Percentage catch	Family	Guild
<i>Eilema depressa/griseola</i>	1	0.2	Erebidae	Lichen
<i>Agonopteryx</i> spp.	3	0.2	Despressariidae	Woody
<i>Agriphila straminella</i>	29	6.5	Crambidae	Grass
<i>Agriphila tristella</i>	20	4.5	Crambidae	Grass
<i>Eilema lurideola</i>	3	0.7	Erebidae	Lichen
<i>Nudaria mundana</i>	3	0.7	Erebidae	Lichen
<i>Abraxas sylvata</i>	2	0.4	Geometridae	Woody
<i>Alcis repandata</i>	1	0.2	Geometridae	
<i>Dysstroma truncata</i>				
<i>truncata</i>	2	0.4	Geometridae	Forbs
<i>Gandaritis pyraliata</i>	1	0.2	Geometridae	Forbs
<i>Geometridae</i> spp.	1	0.2	Geometridae	
<i>Pennithera firmata</i>	1	0.2	Geometridae	Woody
<i>Blastobasis adustella</i>	5	0.2	Blastobasidae	Decay
<i>Catoptria permutatellus</i>	1	0.2	Crambidae	Moss
<i>Perizoma alchemillata</i>	1	0.2	Geometridae	Forbs
<i>Chryosteuchia culmella</i>	12	2.7	Crambidae	Grass
<i>Cilix glaucata</i>	1	0.2	Drepanidae	Woody
<i>Cnephasia</i> spp.	2	0.4	Tortricidae	
<i>Crambus pascuella</i>	1	0.2	Crambidae	Grass
<i>Pug</i> spp.	3	0.7	Geometridae	
<i>Scotopteryx</i>				
<i>chenopodiata</i>	1	0.2	Geometridae	Forbs
<i>Agrotis exclamationis</i>	1	0.2	Noctuidae	Forbs
<i>Amphipoea ocula</i>	2	0.4	Noctuidae	Grass
<i>Amphipoea</i> spp.	1	0.2	Noctuidae	
<i>Amphipyra tragoponis</i>	2	0.4	Noctuidae	Broad
<i>Eudonia lacustrata</i>	5	1.1	Crambidae	Moss
<i>Apamea lithoxyla</i>	1	0.2	Noctuidae	Grass
<i>Gelechiidae</i> spp.	4	0.9	Gelechioidae	
<i>Apamea monoglypha</i>	8	1.8	Noctuidae	Grass
<i>Atethmia centrargo</i>	1	0.2	Noctuidae	Woody
<i>Cerapteryx graminis</i>	9	2	Noctuidae	Grass
<i>Diarsia dahlia</i>	1	0.2	Noctuidae	Woody
<i>Diarsia mendica</i>	2	0.4	Noctuidae	Broad
<i>Diarsia rubi</i>	16	3.6	Noctuidae	Forbs
<i>Hoplodrina</i> spp.	19	4.3	Noctuidae	Forbs
<i>Hydraecia micacea</i>	5	1.1	Noctuidae	Grass
<i>Hydriomena furcata</i>	6	1.3	Noctuidae	Woody

<i>Luperina testacea</i>	1	0.2	Noctuidae	Grass
<i>Mesapamea</i> spp.	86	19.3	Noctuidae	Grass
<i>Mythimna conigera</i>	1	0.2	Noctuidae	Grass
<i>Mythimna impura</i>	21	1.8	Noctuidae	Grass
<i>Mythimna pallens</i>	2	0.4	Noctuidae	Grass
<i>Noctua comes</i>	10	2.2	Noctuidae	Broad
<i>Noctua janthe</i>	2	0.4	Noctuidae	Broad
<i>Plutella xylostella</i>	3	0.7	Plutellidae	Crops
<i>Noctua pronuba</i>	24	5.4	Noctuidae	Grass
<i>Oligia</i> spp.	1	0.2	Noctuidae	Grass
<i>Rivula sericalis</i>	1	0.2	Noctuidae	Grass
<i>Stilbia anomala</i>	1	0.2	Noctuidae	Grass
<i>Tortrix</i> spp.	6	1.3	Tortricidae	
<i>Trichiura crataegi</i>	1	0.2	Lasiocampidae	Woody
<i>Udea lutealis</i>	1	0.2	Crambidae	Forbs
<i>Udea olivalis</i>	1	0.2	Crambidae	Forbs
Unidentified	20	2.5		
<i>Xanthorhoe montana</i>	2	0.4	Noctuidae	Grass
<i>Xestia baja</i>	4	0.9	Noctuidae	Broad
<i>Xestia sextrigata</i>	76	17.1	Noctuidae	Grass
<i>Xestia triangulum</i>	1	0.2	Noctuidae	Broad
<i>Xestia xanthographa</i>	1	0.2	Noctuidae	Grass
<i>Xylena solidaginis</i>	1	0.2	Noctuidae	Woody
<i>Yponomeuta evonymella</i>	1	0.2	Yponomeutidae	Woody
Total	445	100		

Table S.5.4. Frequency of occurrence in quadrats of all plant species (or aggregate groups) recorded

Species (<i>scientific names</i>)	Frequency
Bare ground	20
Bird's foot trefoil (<i>Lotus corniculatus</i>)	4
Bracken (<i>Pteridium aquilinum</i>)	2
Burnet saxifrage (<i>Pimpinella Saxifraga</i>)	1
Buttercup (<i>Ranunculus</i> spp.)	121
Chickweed (<i>Stellaria media</i>)	24

Chicory (<i>Cichorium intybus</i>)	7
Cocksfoot (<i>Dactylis glomerata</i>)	44
Common bent (<i>Agrostis capillaris</i>)	15
Common heather (<i>Calluna vulgaris</i>)	1
Compact rush (<i>Juncus conglomeratus</i>)	2
Creeping bent (<i>Agrostis stolonifera</i>)	1
Crested dogs tail (<i>Cynosurus cristatus</i>)	51
Daisy (<i>Bellis perennis</i>)	22
Dandelion (<i>Taraxacum officinale</i>)	53
Dock (<i>Rumex obtusifolius</i>)	66
Fescue (<i>Festuca</i> spp.)	20
Speedwell (<i>Veronica</i> spp.)	4
Goose grass (<i>Galium aparine</i>)	1
Hawskbeard (<i>Crepis</i> spp.)	6
Heath bedstraw (<i>Galium saxatile</i>)	2
Marsh thistle (<i>Cirsium palustre</i>)	2
Meadowgrass spp (<i>Poa</i> spp.)	136
Moss (<i>Bryophyta</i> spp)	16
Mouse ear chickweed (<i>Cerastium glomeratum</i>)	21
Nettle (<i>Urtica dioica</i>)	4
Oat (<i>Avena sativa</i>)	1
Pineapple weed (<i>Matricaria discoidea</i>)	1
Plantain (<i>Plantago</i> spp.)	36
Ragwort (<i>Senecio jacobaea</i>)	22
Red bartisia (<i>Odontites vernus</i>)	1
Red clover (<i>Trifolium pratense</i>)	4
Red fescue (<i>Festuca rubra</i>)	15
Ryegrass (<i>Lolium</i> spp.)	184
Sedge (<i>Carex</i> spp)	1
Self heal (<i>Prunella vulgaris</i>)	17
Shepherd's purse (<i>Capsella bursa-pastoris</i>)	1
Sorrel (<i>Rumex acetosa</i>)	2
Sweet vernal grass (<i>Anthoxanthum odoratum</i>)	18
Tall fescue (<i>Lolium arundinaceum</i>)	1
Thistle (<i>Cirsium</i> spp.)	31
Timothy (<i>Phleum pratense</i>)	82
Tormentil (<i>Potentilla erecta</i>)	3
Unidentified plant	12
Common vetch (<i>Vicia sativa</i>)	3
White clover (<i>Trifolium repens</i>)	165
Yarrow (<i>Achillea millefolium</i>)	10
Yorkshire fog (<i>Holcus lanatus</i>)	128

Table S.5.5. r^2 values for measures of vegetation composition

Predictor	R2 values ^(a) for response variables				
	Larval abundance	Larval richness	Adult abundance	Adult richness	Adult diversity index
% <i>Lolium</i> spp.	0.04	0.24	0.76	0.19	0.05
Plant diversity index	0.03	0.01	0.2	0.09	0.07
Plant species richness	0.03	0.01	0.05	0.12	0.09

(a). r^2 values reported are marginal r squared as these are more representative of the explanatory power of the fixed effects rather than random effects. Nagelkerke's r squared was used for count data.

Table S.5.6. Model summaries for all models included in model averaging and full models

(Intercept)	date	Grazing intensity (LUs Ha yr)	% <i>Lolium</i> spp.	Sheep (presence)	Treatment	% <i>Lolium</i> spp. x Treatment	Sheep (presence) x Treatment	AICc	delta	weight	r2(marg, cond)
Larval abundance											
<i>Full model</i>											
1.40	0.05	-0.38	0.11	-1.03	-0.18	-0.44	-1.55	241.59	NA	NA	60%, 90%
<i>Reduced models</i>											
1.33	NA	-0.47	NA	+	+	NA	+	233.63	0.00	0.39	59%, 90%
1.26	NA	-0.50	NA	+	NA	NA	NA	233.86	0.23	0.35	54%, 88%
1.49	NA	-0.49	NA	+	+	NA	NA	234.46	0.83	0.26	48%, 89%
Larval richness											
<i>Full model</i>											
0.70	-0.07	-0.28	-0.20	-0.31	-0.19	-0.21	-1.22	147.86	NA	NA	52%, 54%
<i>Reduced models</i>											
0.61	NA	-0.29	-0.32	+	NA	NA	NA	141.98	0.00	0.19	35%, 38%
0.66	NA	-0.28	-0.29	+	+	NA	+	142.05	0.07	0.19	50%, 52%
0.78	NA	-0.37	NA	+	+	NA	+	142.70	0.73	0.13	47%, 52%
0.73	NA	-0.31	-0.29	+	+	NA	NA	143.15	1.17	0.11	38%, 40%
0.64	NA	NA	-0.39	+	+	NA	+	143.16	1.19	0.11	48%, 52%
0.61	NA	NA	-0.42	+	NA	NA	NA	143.32	1.34	0.10	33%, 37%
0.87	NA	-0.40	NA	+	+	NA	NA	143.52	1.54	0.09	35%, 42%
0.70	NA	-0.39	NA	+	NA	NA	NA	143.61	1.63	0.09	31%, 39%
(Intercept)	Temperature	Grazing intensity (LUs Ha yr)	% <i>Lolium</i> spp.	Sheep (presence)	Treatment	% <i>Lolium</i> spp. x Treatment	Sheep (presence) x Treatment	AICc	delta	weight	R ² value

Adult moth abundance												
<i>Full model</i>												
2.99	-0.07	-0.25		-0.14	-0.80	0.17	0.19	0.34	193.40	NA	NA	32%
<i>Reduced models</i>												
NA	2.95		NA	-0.25	NA	NA	NA	NA	172.48	0.00	0.14	15%
-0.57	3.13		NA	NA	NA	NA	NA	NA	172.62	0.15	0.13	15%
-0.55	3.11	-0.21		NA	NA	NA	NA	NA	173.17	0.69	0.10	24%
NA	2.98		NA	NA	NA	NA	NA	NA	173.46	0.98	0.08	0%
NA	2.96	-0.22		NA	NA	NA	NA	NA	173.82	1.35	0.07	10%
-0.38	3.06		NA	-0.18	NA	NA	NA	NA	174.10	1.63	0.06	21%
Adult moth species richness												
<i>Full model</i>												
2.00	-0.03		-0.04	-0.23	-0.29	0.05	0.19	0.06	135.67	NA	NA	29%
<i>Reduced models</i>												
NA	1.98	NA		-0.18	NA	NA	NA	NA	115.86	0.00	0.18	19%
-0.34	2.09	NA		NA	NA	NA	NA	NA	116.82	0.96	0.11	16%
-0.24	2.05	NA		-0.14	NA	NA	NA	NA	117.02	1.16	0.10	25%
(Intercept)	temp_scl	Grazing intensity (LUs Ha yr)	Plant richness	Sheep (presence)	Treatment	Plant richness x Treatment	Sheep (presence) x Treatment		AICc	delta	weight	R ² value
Adult moth diversity												
<i>Full model</i>												
1.71	0.04	-0.05	-0.02	-0.37	-0.02	0.19	0.19		67.99	NA	NA	0%

2.5. Chapter 6: Discussion

Intensive agricultural practices both in Europe and worldwide are a key driver of population declines in a variety of taxonomic groups (Brodie et al., 2021; Grevé et al., 2024; Potts et al., 2010; Reif and Hanzelka, 2020). Intensive agriculture is characterised by landscape simplification through the removal of natural habitat, sowing of crop monocultures and use of synthetic fertilisers, herbicides and pesticides. Whilst agri-environment schemes have been in place for over 30 years in Europe they have done little to halt or reverse widespread biodiversity decline, likely due to their being implemented at field scales. Indeed, there is an increasing recognition within the scientific community that a landscape-scale approach may be necessary to protect and restore biodiversity (Fuentes-Montemayor et al., 2011b; Gámez-Virués et al., 2015; Merckx et al., 2009; Tschardt et al., 2021). Mixed farming may increase landscape heterogeneity (Smith et al., 2020) and reduce synthetic inputs (MacLaren et al., 2019; Nevens and Reheul, 2002). Whilst this could have positive effects for farmland wildlife, the environmental benefits of mixed farming are debated (Rudel et al., 2016; Ryschawy et al., 2012b), with the integration of livestock with crops sometimes leading to further intensification (Regan et al., 2017). I collected and analysed data on nocturnal insects and bat activity across 26 farms in East Scotland (13 mixed and 13 arable, chapters two to four) in order to assess the direct and indirect effects of mixed farming on nocturnal invertebrates and bats. To my knowledge this is the first time that the overall effects of mixed farming on bats and nocturnal invertebrates have been assessed in comparison to arable farming. My study taxa included the poorly studied micro moths (chapter two), adding to a limited pool of knowledge on local and landscape attributes that are important for this group of insects. Furthermore, I investigated the effects of farming type on bat activity at two different times of year: summer and autumn, providing valuable information on local and landscape attributes that are important for bats during the pre-

hibernation period (chapter four), an area of research that has received little attention.

High livestock stocking rates and intensive pasture management practices may limit the ability of livestock systems to benefit biodiversity and can even be detrimental to invertebrates in comparison to less intensively managed pastures or ungrazed areas (Littlewood, 2008; Pöyry et al., 2004). I therefore investigated the potential for a regenerative grazing practice: mob-grazing to increase moth abundance and diversity in comparison to set-stock grazing in chapter five, using data collected across another 26 farms in Scotland. To my knowledge this is the first time that moth abundance and diversity have been compared between these two farming systems. In addition, I focussed on the response of moth larvae, which has rarely been covered in the literature, with results showing the benefits of using this life cycle stage for understanding the effects of field-scale management on moths.

My research has started to fill knowledge gaps on the impacts of mixed farming and regenerative grazing on biodiversity. My findings are relevant to both farmers seeking to increase biodiversity and are especially timely for policy makers designing the latest Agri-Environment Climate Schemes (AECS) in Scotland and Environmental Land Management Schemes in England. Findings are also applicable to other temperate agricultural landscapes across the globe.

6.1. Is mixed farming beneficial for bats and nocturnal insects overall?

6.1.1. A mismatch of scales

An important focus of my research was to disentangle direct and indirect effects of farm type (mixed or arable) on biodiversity, with indirect effects being potentially mediated by landscape attributes and/or local features. Indeed, mixed farming has the potential to influence landscape

features, for example by increasing landscape heterogeneity through the addition of pasture habitat that is lacking on arable farms, or by retaining woodlands as shelter for livestock. As well as disentangling direct and indirect effects, I aimed to understand the overall impacts of mixed farming. In Chapters two to four I found that farm type was significantly associated with certain landscape attributes but not always at scales that were relevant to study species. Mixed farms had significantly higher habitat diversity than arable farms, but only at smaller scales of 250 and 500 m radius from moth traps/ bat detectors. Of all landscape metrics considered, habitat diversity index was most strongly correlated with the proportion of arable at the same scales (Pearson = - 0.8, - 0.9). As such, it is likely that arable farms are reducing the diversity of habitats available by dedicating a greater proportion of the farm to crop fields. Whilst mixed farming was positively associated with higher habitat diversity at small scales (Figure. 6.3), habitat diversity was not a strong predictor (mostly marginally non-significant) of any of the taxonomic groups in my study. In addition, where there was a weak association, this was found at much larger scales of 2000-m radius for *P. pipistrellus* in the autumn and 1000 m for Hymenoptera abundance. Thus, there appears to be a mismatch between the scales of habitat diversity relevant for bats and nocturnal insects, and the scales at which mixed farming is associated with higher habitat diversity (Figure 6.2.). Farms in this study were on average 200 ha in size so their management was unlikely to influence landscapes at scales greater than around 1500-m radius (from the centre of the farm). Collaborative projects between multiple farms may be more effective at increasing landscape heterogeneity at larger scales that are relevant to *P. pipistrellus* and Hymenoptera. This may be particularly relevant for UK farms as the average farm size of 86 Ha (UK Government, 2024) is much smaller than the mean farm size in my study (200 Ha). Collaborations between farmers with the aim of reversing population declines of meadow birds in agricultural areas have been used with moderate success in the Netherlands (Runhaar and Polman, 2018).

Greater woodland edge density was also associated with mixed farming, but this time at larger scales of 1500 and 2000 m (and marginally at 1000 m). Woodland edge density was only slightly negatively correlated with the proportion of arable cover (Pearson = - 0.6). Thus, in my study sites the amount of woodland edge doesn't appear to be strongly driven by the proportion of arable. As such, it is difficult to draw conclusions on the association between woodland edge density and farm type. It is possible that arable farmers tend to select areas that are highly fertile and may have been subjected to woodland removal in the past, with farmers practising mixed farming able to make use of less productive soils (where woodlands may not have historically been removed to such an extent due to less favourable soil for crops). Interestingly, both *P. pipistrellus* and micro moths responded positively to increased woodland edge density at smaller scales than those associated with mixed farming, again highlighting a mismatch of scales.

Whilst there was a clear mismatch of scales for some taxonomic groups, mixed farming did have a significant positive effect on *Myotis* occurrence and a marginally non-significant positive effect on micro moth abundance and species richness mediated by woodland edge density on mixed farms at the 1000 and 1500-m scales. Higher habitat diversity associated with mixed farming at smaller scales (250 m) marginally increased the diversity of insect orders.

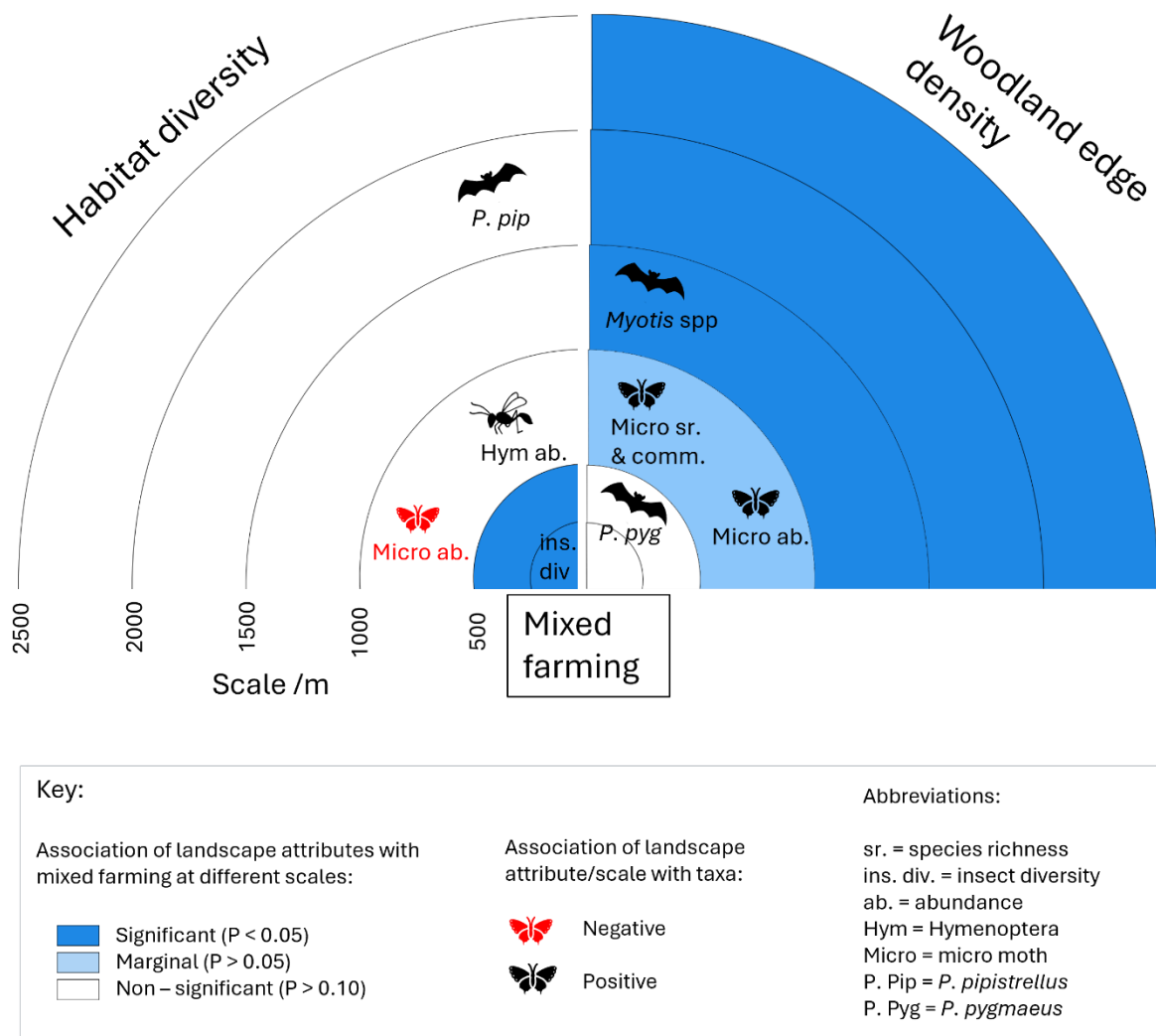


Figure 6.1. Infographic summarising indirect effects of mixed farming mediated by landscape attributes at scales from 250 m to 3000 m. Where a taxonomic group is placed within a landscape band, this shows a significant association between that landscape attribute (habitat diversity or woodland edge density) at that specific scale. Coloured bands show a significant (dark blue) or marginal (light blue) associated between mixed farming and a specific landscape attribute (woodland edge density or habitat diversity) at a specific scale.

6.1.2. Overall effects of mixed farming

One of the key aims of this thesis was to understand the overall effects (combination of direct and indirect pathways) of mixed farming on bats and invertebrates. I only found a significant overall benefit of mixed farming for *Myotis* spp. occurrence, with an overall marginal positive effect on micro moth abundance, insect diversity and Trichoptera abundance. However, the overall

effect of mixed farming was negative for Brachycera and marginally negative for micro moth species richness and *Pipistrellus* spp. activity. In addition, where significant overall positive effects of mixed farming were found the effect size was very small.

The lack of any strong overall positive effects of mixed farming for biodiversity could be because the integration of livestock with crops alone is not enough to reduce intensive farming practices. Indeed, none of the farms in my study were organic and as such were likely using insecticides and synthetic fertilisers on a frequent basis. Whilst I was unable to obtain information on fertiliser applications for all farms, for those that did provide accurate information (n arable = 6, n mixed = 5), mixed farms did not seem to be reducing their fertiliser inputs compared with arable farms (Table S.2.4). Thus, more research is needed to understand if mixed farming does in fact reduce synthetic inputs.

Furthermore, mean stocking rate on the mixed farms used in this study (2.4 LUs per Ha) has been associated with lower insect abundance and diversity than lower stocking rates (Jerrentrup et al., 2014). Furthermore, all mixed farms in my study were using anthelmintic wormers which are known to be detrimental to invertebrates (Manning et al., 2018). Therefore, intensive pasture management could be another underlying cause of the lack of any benefits of mixed farming. In fact, I found no increase in insect abundance or diversity adjacent to pasture fields, which is different to other studies (Evans et al., 2007). For mixed farming to be beneficial, it may need to be combined with other regenerative agricultural practices such as no-till (where arable seeds are drilled directly into the ground, avoiding the ploughing of fields and disturbance of soil biota) and reduced use or cessation of insecticides, synthetic fertilisers and anthelmintic wormers. Though regenerative farming practices like these are on the increase, more research is needed to support (or otherwise) their combined benefits for the environment (Musto et al., 2023).

6.2. Importance of landscape attributes for different taxonomic groups

Preserving biodiversity on farms is a complex challenge, since the needs of many different species need to be taken into account. Previous studies have found that different taxonomic groups can respond similarly or differently to the same management practice. For example AES had opposing effects on moths and bats (Fuentes-Montemayor et al., 2011a, 2011b) and plants, parasitoids and birds respond differently to agricultural intensity in grassland systems (McMahon et al., 2012). In Chapters two and four I found that woodland edge density was an important predictor of activity of *P. pygmaeus* and occurrence of *Myotis* spp., as well as micro moth abundance and species richness and to a lesser extent micro moth community composition. The similar positive response to woodland edge density by bats and micro moths (even for farmland micro moths that don't feed on woody plant species) suggests that increasing woodland edge density on farms can have benefits for both predators and prey. Whilst the bat species most commonly recorded in my study area mainly feed on Diptera, with moths only making up a small proportion of their diet (Swift et al., 1985), increasing moth abundance on farmland may have important benefits for moth-feeding bats that are present in agricultural land in more southern parts of the UK.

Increasing habitat edge density can be a symptom of habitat fragmentation, particularly when comparing areas of higher forest edge density with those where large areas of forest are still intact (Broadbent et al., 2008). However, on my sites woodland edge density positively correlated with the proportion of woodland at the same scales (Pearson 0.4 – 0.75). In addition, areas with high woodland edge density also had woodland patches that were closer together (as measured by mean woodland Euclidean Nearest Neighbour). As such in my study area woodland edge density is associated with agricultural landscapes with more woodland, even if that woodland is

fragmented. Increasing woodland on farms can cause conflicting priorities for farmers who can be reluctant to give up productive land (Felton et al., 2023). However, I found important increases in moth abundance and bat activity associated with very small increases in woodland edge density, with micro moth abundance increasing by 30 % with every additional 20 m of woodland edge per Ha and the activity of *P. pygmaeus* increasing by 20 % with the same increase in woodland edge. Provision of more woodland could be particularly important for *Myotis* spp., with an increase of 20 m woodland edge associated with an 80 % higher chance of recording this group. The amount of additional woodland edge associated with these substantial increases in bat activity and occurrence and moth abundance is very small and unlikely to lead to large losses in crop production. In fact, woodland on farms can increase beneficial invertebrate predators, potentially reducing crop damage from herbivorous insects (Kolkert et al., 2021). Woodlands created on agricultural land are capable of providing habitat for Diptera (Fuller et al., 2018) and small mammals (Fuentes-Montemayor et al., 2020) even when they are relatively young.

Even if farmers are reluctant to dedicate productive land for woodland creation/ expansion, woodland can be used as pasture for livestock, particularly during winter months when drier ground or shelter may be needed (or during heatwaves in warmer climates) and may not necessarily lead to a loss in income for the farm. However, grazed woodlands may harbour different moth communities (Fuentes-Montemayor et al., 2022) and can even reduce moth abundance and species richness (Fuentes-Montemayor et al., 2012), with negative impacts also found for some mammal species such as wood mice and bank voles (Fuentes-Montemayor et al., 2020) and ground-dwelling invertebrates (Lindsay and Cunningham, 2009) in comparison to ungrazed woodland. Conversely, positive effects of grazed wooded areas compared to ungrazed have been seen for bats (Edo et al., 2025; Fuentes-Montemayor et al., 2013). It is important to note that all of these studies only accounted for the presence or absence of grazing in woodland sites and further research is

needed on the effects of different stocking rates in woodland pasture on biodiversity.

Alternatively, woody features may be incorporated into the farm through silvoarable practices where arable crops and trees are integrated, though this is more common in tropical areas, where trees are integrated with the aim of providing shade for crops such as coffee plants (Ongole et al., 2018). These silvoarable areas can provide foraging habitat for bats (Ongole et al., 2018) who in turn provide pest-regulation services for crops (Sow et al., 2020). Woodland edge may also be incorporated onto farmland via orchards/ plantations that can also provide foraging areas for bats (Maas et al., 2013). However, whilst silvoarable practices provide habitat for some species, there is lack of research that compares the value of silvoarable areas with native woodlands for biodiversity (Mupepele et al., 2021)

Habitat diversity tended to positively affect a range of study groups, though the effect was only ever marginally significant. Hymenoptera, the overall diversity of insect orders and *P. pipistrellus* in the autumn all increased with increasing landscape heterogeneity. However, micro moth abundance was significantly negatively associated with areas of higher habitat diversity, though this could be because areas with high habitat diversity (and more woodland) creates barriers to movement for less mobile species.

The main land-use types in my study area were arable fields, pasture, woodland (all woodland types combined), freshwater and buildings. Habitat diversity showed the strongest correlation with the proportion of arable (negative, Pearson $r > -0.8$ at all scales) and a slight positive correlation with woodland edge density at some scales (Pearson 0.5 – 0.7 depending on scale). There was no correlation between habitat diversity and the proportion of pasture. Thus, it seems that low habitat diversity in landscapes in my study was likely driven by greater proportions of arable farming in the landscape, similarly to (Holzschuh et al., 2007). The positive effects of habitat diversity across

different taxonomic groups may be in part due to a lower proportion of the surrounding landscape being under intensive agriculture.

The fact that I only found a weak positive effect of habitat diversity on moths and bats could be due to how intensively farmed this part of Scotland is. Indeed, my study area is dominated by arable crops (mean cover at 3000 m = 45 %, min = 20 %, max = 74 %). East Scotland is a particularly high-yielding area for cereals and an important area for potato growing (Kilpatrick et al., 2008). Both cereal crops and potatoes require high levels of fertiliser in comparison to improved grassland (National Statistics, 2023; Table S.6.1) and high levels of pesticides are applied in particular to oilseed rape and potatoes in the UK (Ridley et al., 2022). Indeed, intensively farmed homogenous agricultural landscapes can reduce the effectiveness of agri-environment schemes and semi-natural patches to increase biodiversity on farmland (Concepción et al., 2012; Xu et al., 2025).

Table S.6.1. Average field rates (2018 – 2022) of total nitrogen (kg/Ha) applications in Great Britain on different crops and improved grassland^a

	Winter wheat	Spring barley	Potatoes	Oilseed rape	Improved grassland
Total nitrogen	183	100	146	173	90

^a Using data from (National Statistics, 2023)

6.3. Importance of linear woody features for different taxonomic groups

Taller woody feature heights were associated with higher abundance and diversity of a variety of taxonomic groups studied across chapters two to four.

Woody feature height was a particularly important predictor for bat activity and occurrence, with activity of *Pipistrellus* spp. increasing between 11 and 23% with a relatively small (2 m) increase in woody feature height (woody features on my sites were on average 14 m high and ranged from 1.7 m to 35 m). *Myotis* spp. occurrence was also marginally positively affected by woody feature height. The main insect group in *Pipistrelle* diet (Nematocera) was unaffected by woody feature height. However, the abundance of some insect orders responded positively to woody feature height (Lepidoptera, Trichoptera, Brachycera), similarly to *Pipistrelles*. Whilst these insects are not a main component in *Pipistrelle* or *Myotis* spp. diet they are consumed in small quantities (around 15 % of *Pipistrelle* diet when combined), particularly Brachycera and Trichoptera (Barlow, 1997). Farmland micro moth abundance increased by 4.5 % with every 2 m increase in woody feature height with farmland micro moth species richness and diversity also marginally positively associated with taller woody features. Brachycera abundance was only slightly higher adjacent to taller woody features. With an increase of 2 m in height increasing Brachycera abundance by just 1.5 %. This is similar to findings in (Froidevaux et al., 2019) where reduced trimming regimes (leading to taller hedgerows) increased abundance of insect prey and bat activity. Thus, increasing the height of hedgerows and treelines on farms will not only directly benefit bats, likely by providing sheltered foraging areas, but may also benefit moth-feeding bats by increasing the abundance of insect prey (although I found very little increase in the abundance of other *Pipistrelle* prey groups).

Community composition of both macro and micro moths was significantly different across a gradient of woody feature height. Different moth species are known to fly at different heights (De Smedt et al., 2019). Thus, changes in community composition across a gradient of woody feature height could be due to some higher-flying moth species using taller woody features but not lower features. However, I recognise that my estimate of woody feature height may be driven by various factors that were not measured in this study,

such as trimming regime and age of hedges and tree lines that can both affect insect abundance and bat activity (Froidevaux et al., 2019a; Froidevaux et al., 2019b). Additionally, taller woody features were significantly associated with the presence of certain tree species, such as conifers (*Picea* spp.) and sycamores (*Acer pseudoplatanus*), with lower woody features significantly associated with low growing plant species such as gorse (*Ulex europaeus*) dog rose (*Rosa canina*) and hawthorn (*Crataegus monogyna*). Differences in hedgerow plant composition and structural diversity can affect micro moth community composition (Boutin et al., 2011b; Froidevaux et al., 2019) likely by providing different foodplants and micro climates. This highlights that whilst taller woody features can benefit a variety of taxa, it is also important to consider diversity in the character of linear woody features (e.g. hedgerows composed of lower-growing woody plant species and lines of trees) which may contribute to increasing beta diversity at the farm scale.

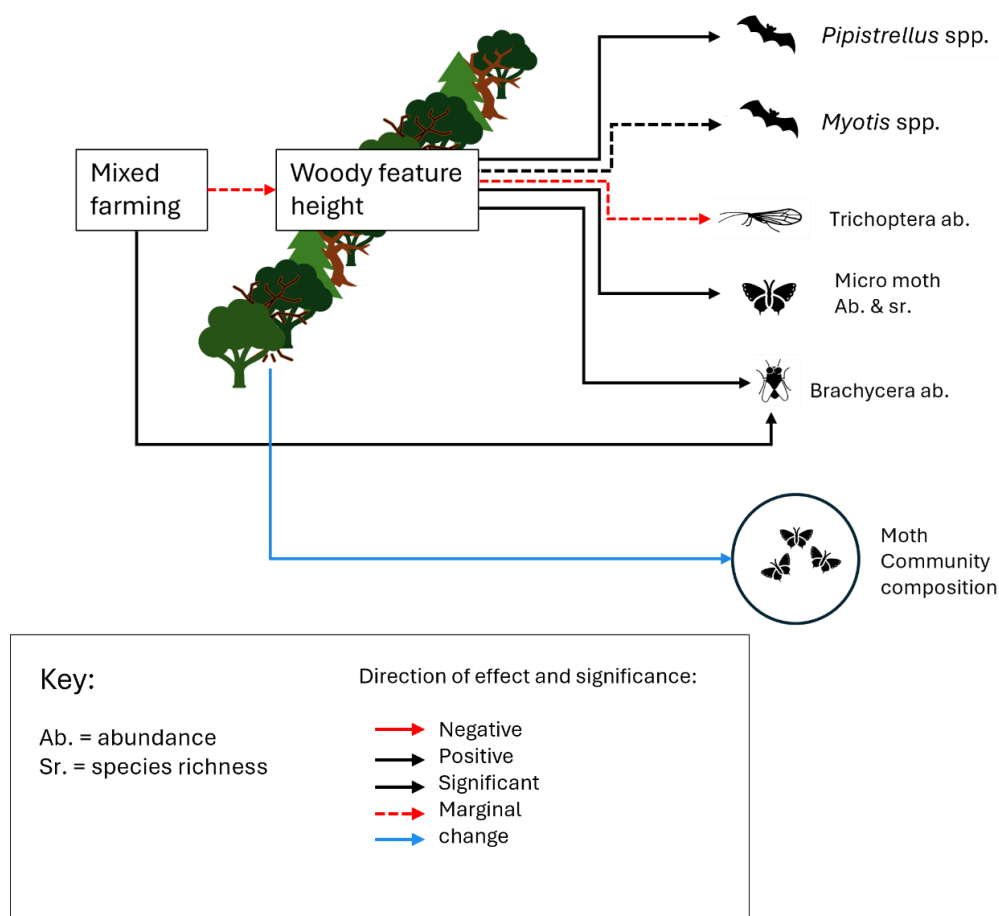


Figure 6.2. Summary of the effect of woody feature height across different taxonomic groups.

6.4. Effects of stocking rate on mixed farms

The impacts of livestock management on mixed farms on bats and nocturnal invertebrates were investigated across chapters three and four. On mixed farms, I assessed the effect of whole-farm cattle stocking rate (number of livestock units divided by the total area of grazing available on the farm – $\text{LUs}^{-1} \text{Ha}^{-1}$) on bats (chapter four) and nocturnal insects (chapter three). Overall, higher stocking rates on mixed farms had either no effect or a negative effect on invertebrates. Stocking rate on mixed farms was negatively associated with Hymenoptera and Trichoptera abundance (chapter three). The effects of the presence of sheep grazing on invertebrates were also assessed in chapters two to four. Sheep grazing had a negative effect on the abundance and species richness of moths in chapter two and on the abundance of Brachycera on mixed farms in chapter three.

Conversely, *Pipistrellus* spp. activity was positively affected by cattle stocking rate on mixed farms, with *P. pygmaeus* also responding positively to sheep grazing (though the increases in activity were only small). However, these positive effects of stocking rate and sheep grazing were only found in the autumn, with no effect found in the summer. This is most likely because insects are abundant across a range of habitats during the summer months but are scarcer in the autumn. In fact, bats are known to be able to track concentrated insect resources and make opportunistic use of 'outbreaks' of insects (McCracken et al., 2012). Whilst I was not able to collect data on bat prey in the autumn, I found no significant effect of stocking rate on the main food groups of bats during the summer months (Nematocera and Brachycera). Whilst I investigated the effects of stocking rate across the whole-farm, Diptera are likely more localised and affected by microclimates and local features (e.g. if cattle are present nearby rather than somewhere else on the farm).

6.5. Benefits of a regenerative grazing practice: mob-grazing

The negative effects of stocking rate on invertebrates and the lack of any benefit of pasture on mixed farms led me to investigate different pasture management practices that could be beneficial for nocturnal invertebrates. In chapter five, I compared moth abundance and diversity in mob-grazed and set-stock fields. Mob grazing is suggested to be beneficial for biodiversity by increasing pasture rest period and reducing the length of time that cattle spend in an area. Indeed, in my study, mob-grazing was positively associated with taller vegetation and longer pasture rest times.

I found no direct benefit of mob grazing for adult moths compared with set-stock fields. However, caterpillar abundance and species richness was lower in set-stock fields that had the additional pressure of sheep grazing, whilst abundance and species richness of caterpillars were not significantly different between in mob-grazed fields with sheep and without sheep. This suggests that mob grazing is mitigating the negative effects of sheep-grazing, most likely due to longer pasture rest times increasing vegetation height, so that grazing sheep has less of an impact on moths.

Higher grazing intensity in both mob-grazed and set-stock fields was negatively associated with abundance and species richness of moth larvae. Interestingly, mean year-round grazing intensity was similar between mob-grazed and set-stock fields, suggesting that farmers practising mob grazing are not making sacrifices with regards to the numbers of cattle they are able to keep in a given area across the year.

6.6. The context of future agricultural policies and trends in farming

For the past three decades, agri-environment schemes have been the main government policies in Europe aimed at increasing wildlife on farms, with similar policies implemented in the USA and New Zealand. These action-based government-led schemes remunerate farmers for implementing certain management practices that are thought to be beneficial for wildlife. This current approach has been criticised by farmers for its lack of flexibility (Emery and Franks, 2012) and research has highlighted a lack of success in benefitting highly mobile species (Batáry et al., 2015). Indeed, farmers are remunerated for implementing actions regardless of whether or not the scheme was successful in increasing abundance/diversity of the target species (or species group). Results-based payments are farmer-led initiatives where farmers are remunerated for a proven increase in biodiversity (or presence of a target species) on their farm, regardless of the management practices used to achieve this. Results-based payments are on the increase in Europe and whilst uptake is low, this approach appears to be successful in its outcomes for biodiversity (Hagemann et al., 2024) (Elmiger et al., 2023). In England, part of the new Environmental Land Management Scheme is based on results-based landscape-scale recovery of biodiversity (though part of this will be privately funded rather than Government funded). In a pilot study in England, farmers increased biodiversity to a greater extent using a trial result-based scheme than farmers implementing agri-environment schemes (Chaplin et al., 2021). Farmer-led nature conservation (whilst not financially encouraged by governments) has also been successful in Tanzania (Moore et al., 2020). Farmers with more experience in environmental management or more wildlife-friendly motivations can also have more successful outcomes of AES (McCracken et al., 2015). This shows that farmer-led initiatives are potentially a valuable tool in tackling biodiversity loss on farmland.

The two management practices studied in this thesis (mixed farming and mob-grazing) are currently not supported by AES and are largely farmer-led initiatives. Key motivations of farmers for implementing mixed farming systems is to stabilise and diversify income, but also to enhance ecosystem services (with likely benefits for biodiversity), with almost half of farmers in a survey carried out in France mentioning environmental stewardship as a key motivation (Meunier et al., 2024). Similarly, mob-grazing is often implemented with the aim of improving cattle health, but motivations can also be environmental, such as increasing soil organic matter or biodiversity in pastures (Wagner et al., 2023). Whilst results from this thesis can help to inform top-down action-based policies, they can also add to the growing body of evidence for the effectiveness (or otherwise) of farmer-led nature restoration and help to inform farmers on the effectiveness of mixed farming and mob-grazing for increasing biodiversity.

A key finding from this research, was the consistent positive response of various taxonomic groups to increasing hedgerow height. Current agri-environment climate schemes in Scotland encourage retention of hedgerow trees and filling of gaps as well as having restrictions on the frequency and timing of hedge trimming under the 'management and restoration of hedgerows' scheme, which could lead to taller hedgerows. However, there is currently no clear AECS management that rewards taller hedgerows. In fact, for a hedgerow to qualify for the 'management and restoration' scheme it only needs to be a minimum of 1.5 m tall (liner woody features in my study ranged from 1.7 to 35 m tall). Furthermore, whilst hedgerows continue to be protected by the 'Management of Hedgerows 2024' in England (prohibiting trimming between 1st March and 31st August) and the Wildlife and Countryside act in the UK (prohibiting the removal of hedgerows over 20 m long), there is no policy that governs how regularly hedgerows can be trimmed (or by how much).

The mismatch of scales at which the farms in this study operated and those relevant to bats highlights the need for greater collaboration between

farmers to increase habitat diversity at a landscape scale. This could be done, for example, by neighbouring farmers co-ordinating the provision of different habitat types at the landscape scale or by co-ordinating habitat creation to provide better connectivity as has been done in the Netherlands (Runhaar and Polman, 2018) . However, the Common Agricultural Policy (CAP) in Europe has been criticised in its approach at targeting individuals and preventing collaboration between farmers (Leventon et al., 2017)

Until 2021, UK agricultural policy was regulated by the CAP, and AES have been the main approach to increasing biodiversity on farms. However, since the UK left the European Union in 2021, there has been a need for new farmland regulations. In England, AES have been replaced with the Environmental Land Management Scheme, which is in the process of being rolled out. There are three key components of this scheme:

1. The Sustainable Farm Incentive: this is similar to former AES and provides farm-level management options that are monitored over a three to five year period. Farms can be clustered to claim rewards from this scheme which could encourage more collaboration between farmers.
2. The Countryside Stewardship Plus: These are more complex management options aimed at the farm-level and monitored over a five year period.
3. The Landscape Recovery scheme: This is meant to encourage collaborations between landowners and has the potential to encourage landscape-scale conservation,

Whilst parts of these schemes have the potential to increase collaborations between farmers, with possible landscape-scale habitat restoration, concerns have been raised over the lack of flexibility, mainly due to long-term monitoring required under the Landscape Recovery Scheme (Dewally et al., 2025). In Scotland, agri-environment climate schemes are in the process of being

phased out. However, it is unclear whether new schemes will have a collaborative element similar to the 'Landscape Recovery Scheme'.

6.7. Complementarity and limitations of survey methods for bats and nocturnal invertebrates

6.7.1. Bats

Acoustic recordings of bat echolocation calls are an inexpensive method to quantify bat activity. Whilst this method cannot quantify bat populations or numbers (as multiple passes recorded may be due to multiple bats flying past a detector, or one bat passing by multiple times), for the species that were most active in the study area (*P. pipistrellus* and *P. pygmaeus*) there is a positive relationship between bat activity and relative abundance. Acoustic methods are also effective at determining presence of *Myotis* spp. (Lintott et al., 2014).

In chapter four two methods were used to record bat activity 1. Walked transects with a hand-held recording device on a single night and 2. Deploying detectors in a fixed position (static) that were left to record for several nights. Both methods are widely used in the literature for quantify bat activity, although static detectors are considered more standardised (Stahlschmidt and Brühl, 2012a) but depend strongly on their location (e.g. quality of feature where they are placed) and may miss activity occurring elsewhere in the study area. Transects can cover a larger area and more habitat types but are restricted in the amount of time spent in each habitat type. In addition, overall survey time is shorter reducing the probability of recording species that are scarce or difficult to detect such as brown long-eared bats (*Plecotus auritus*). I used two different survey methods to answer two different questions:

1. Transects to assess habitat preferences of bats on arable and mixed farms, with transects enabling me to cover a range of different habitat types across the farm.
2. Static detectors to assess the direct and indirect effects (mediated by local features and landscape attributes) of mixed farming. This method allowed a greater sample size ($n = 104$ locations across 26 farms) compared with transects ($n = 20$ farms) allowing for enough variation in landscape attributes to conduct landscape analysis.

There have been a number of studies comparing these two methods with a general agreement that static detectors are able to record higher species richness than walked transects, likely because of being deployed for the whole night (Green et al., 2024; Perks and Goodenough, 2021; Teets et al., 2019). However, in Europe walked transects detected greater activity of *Plecotus auritus* and *P. pygmaeus* (Perks and Goodenough, 2021) potentially due to covering more habitat types that may be used by these two specialist species. Another comparison showed that transects can produce data with a greater standard error than static detectors (Stahlschmidt and Brühl, 2012b), most likely due to less data recorded during transects (from a shorter recording period). Interestingly, in my study results obtained from transects were supported by results from static detectors. For example, I found preferential use of woodland by *P. pygmaeus* and buildings by *P. Pipistrellus* using both methods. However, transect surveys often missed the occurrence of *Myotis* spp. in comparison to static detectors (occurrence on transects = 5/20 farms, occurrence in static recordings = 23/26 farms). In addition, static detectors recorded a small number of *Plecotus auritus* passes which were not detected on any farms using transect methods, which supports findings from Green et al. (2024) that increasing length of recordings increases the probability of recording less common bat species. Thus, static detectors, particularly when deployed at different locations across a site, are a better option when wanting to record less common or quieter species. However, for

assessing the importance/use of different habitat features by common species, either method can be used as long as enough static detectors are deployed to cover a range of habitats.

6.7.2. Moths

Many studies that assess the effects of environmental variables on moths focus on surveys of adult moths using light trapping. In chapter 5, I used both light trapping of adult moths combined with larval surveys (which included both butterfly and moth species). I found significant effects of grazing intensity, sheep grazing and the proportion of ryegrass cover for caterpillars but found no significant effects on adult moths. In addition, models for adult moths explained less variation in the data than those for Lepidoptera larvae. Thus, had I not surveyed for caterpillars I would not have picked up on the importance of pasture management practices for moths. The lack of significant findings for adult moths is likely due to their high mobility (particularly macro moths). Around half of the adult moth species found in light traps were woody plant-feeding species, so they are likely to have travelled to the light trap from habitats outside of the pasture where the trap was set. Moths can be affected by landscape composition up to distances of 1km from traps (Fuentes-Montemayor et al., 2011a; Kühne et al., 2022). Thus, larval sampling may be a better measure of small spatial scale effects than trapping adult moths, although the former is more labour-intensive and did not enable the comparison of communities of caterpillars due the low number of species/abundance caught (total species = 18; total abundance = 218), whereas this was possible with data from light traps (total species = 60; total abundance = 434).

6.8. Management recommendations

Management recommendations that can be drawn from the findings of this thesis are:

1. Increasing woodland edge on farms (via creating new woodlands or expanding woodland area) can benefit both bats and moths.
2. Increasing hedgerow/ tree line height can benefit bats, moths and Brachycera. On mixed farms, it should be ensured that livestock are not negatively impacting on the quality of hedgerows either via browsing or hedgerow trimming for use as livestock barriers.
3. Buildings are important for *P. pipistrellus* and should be managed in a way that reduces negative impacts on bats (e.g. less lighting around buildings (Mathews et al., 2015b)). However, this should be done in combination with reduced insecticide use around farm buildings and less intensive farming practices in the surrounding landscape to avoid creating ecological traps.
4. Increasing habitat diversity at scales that are most relevant to *P. pipistrellus* may be achieved by collaborations between neighbouring farms.
5. On farms where both cattle and sheep are grazed, mob-grazing can help to reduce grazing pressure from sheep, increasing moth abundance and species richness compared with set-stocking of cattle. Furthermore, mob-grazing did not require a reduction in livestock density across the year compared with set-stocking, so farmers would not need to reduce numbers of cattle on the farm.
6. Reducing grazing intensity and favouring lower input pasture (with lower cover of ryegrass) can benefit grassland moths. However, higher numbers of cattle may provide a small source of insects in the autumn for bats feeding up prior to hibernation (though the benefits of

increasing livestock stocking rate levelled off at around 2.5 LUs Ha⁻¹ for *P. pygmaeus*).

References

- Abson, D.J., 2019. Chapter 19 – The Economic Drivers and Consequences of Agricultural Specialization, in: Lemaire, G., Carvalho, P.C.D.F., Kronberg, S., Recous, S. (Eds.), *Agroecosystem Diversity*. Academic Press, pp. 301–315. <https://doi.org/10.1016/B978-0-12-811050-8.00019-4>
- Afonso, E., Tournant, P., Foltête, J.-C., Giraudoux, P., Baurand, P.-E., Roué, S., Canella, V., Vey, D., Scheifler, R., 2016. Is the lesser horseshoe bat (*Rhinolophus hipposideros*) exposed to causes that may have contributed to its decline? A non-invasive approach. *Glob. Ecol. Conserv.* 8, 123–137. <https://doi.org/10.1016/j.gecco.2016.09.002>
- Agassiz, D.J.L., Beavan, S.D., Heckford, R.J., 2024. A checklist of the Lepidoptera of the British Isles, Second Edition. *Br. Entomol. Nat. Hist. Soc.* <https://doi.org/ISBN:%2520978-1-899935-10-9>
- Aguilera, G., Roslin, T., Miller, K., Tamburini, G., Birkhofer, K., Caballero-Lopez, B., Lindström, S.A.M., Öckinger, E., Rundlöf, M., Rusch, A., Smith, H.G., Bommarco, R., 2020. Crop diversity benefits carabid and pollinator communities in landscapes with semi-natural habitats. *J. Appl. Ecol.* 57, 2170–2179. <https://doi.org/10.1111/1365-2664.13712/FORMAT/PDF>
- AHDB, n.d. Mob grazing, what's it all about?
- Aldasoro, M., Garin, I., Vallejo, N., Baroja, U., Arrizabalaga-Escudero, A., Goiti, U., Aihartza, J., 2019. Gaining ecological insight on dietary allocation among horseshoe bats through molecular primer combination. *PLOS ONE* 14, e0220081. <https://doi.org/10.1371/journal.pone.0220081>
- Aldridge, H.D.J.N., Rautenbach, I.L., 1987. Morphology, Echolocation and Resource Partitioning in Insectivorous Bats. *J. Anim. Ecol.* 56, 763–778. <https://doi.org/10.2307/4947>
- Al-Kaisi, M.M., Lal, R., 2020. Aligning science and policy of regenerative agriculture. *Soil Sci. Soc. Am. J.* 84, 1808–1820. <https://doi.org/10.1002/saj2.20162>
- Ancillotto, L., Ariano, A., Nardone, V., Budinski, I., Rydell, J., Russo, D., 2017. Effects of free-ranging cattle and landscape complexity on bat foraging: Implications for bat conservation and livestock management. *Agric. Ecosyst. Environ.* 241, 54–61. <https://doi.org/10.1016/j.agee.2017.03.001>
- Ancillotto, L., Labadessa, R., Roscioni, F., Montioni, F., Fulco, E., Zollo, L., Spilinga, C., 2023. Protected habitats support bats in Mediterranean dry grasslands. *Sci. Total Environ.* 882, 163415. <https://doi.org/10.1016/j.scitotenv.2023.163415>
- Anderson, M., Rotheray, E.L., Mathews, F., 2023. Marvellous moths! pollen deposition rate of bramble (*Rubus futicosus* L. agg.) is greater at night than day. *PLOS ONE* 18, e0281810. <https://doi.org/10.1371/journal.pone.0281810>

- Anderson, M.E., Racey, P.A., 1993. Discrimination between fluttering and non-fluttering moths by brown long-eared bats, *Plecotus auritus*. Anim. Behav. 46, 1151–1155. <https://doi.org/10.1006/anbe.1993.1304>
- Andriollo, T., Gillet, F., Michaux, J.R., Ruedi, M., 2019. The menu varies with metabarcoding practices: A case study with the bat *Plecotus auritus*. PLoS ONE 14. <https://doi.org/10.1371/journal.pone.0219135>
- Antão, L.H., Weigel, B., Strona, G., Hällfors, M., Kaarlejärvi, E., Dallas, T., Opedal, Ø.H., Heliölä, J., Henttonen, H., Huitu, O., Korpimäki, E., Kuussaari, M., Lehikoinen, A., Leinonen, R., Lindén, A., Merilä, P., Pietiäinen, H., Pöyry, J., Salemaa, M., Tonteri, T., Vuorio, K., Ovaskainen, O., Saastamoinen, M., Vanhatalo, J., Roslin, T., Laine, A.-L., 2022. Climate change reshuffles northern species within their niches. Nat. Clim. Change 12, 587–592. <https://doi.org/10.1038/s41558-022-01381-x>
- Apfelbaum, S.I., Thompson, R., Wang, F., Mosier, S., Teague, R., Byck, P., 2022. Vegetation, water infiltration, and soil carbon response to Adaptive Multi-Paddock and Conventional grazing in Southeastern USA ranches. J. Environ. Manage. 308, 114576. <https://doi.org/10.1016/j.jenvman.2022.114576>
- Arbuckle, B.S., Price, M.D., Hongo, H., Öksüz, B., 2016. Documenting the initial appearance of domestic cattle in the Eastern Fertile Crescent (northern Iraq and western Iran). J. Archaeol. Sci. 72, 1–9. <https://doi.org/10.1016/j.jas.2016.05.008>
- Arnold, T.W., 2010. Uninformative Parameters and Model Selection Using Akaike's Information Criterion. J. Wildl. Manag. 74, 1175–1178.
- Aspinall, R., Staiano, M., 2019. Ecosystem services as the products of land system dynamics: lessons from a longitudinal study of coupled human–environment systems. Landsc. Ecol. 34, 1503–1524. <https://doi.org/10.1007/s10980-018-0752-7>
- Aune, S., Bryn, A., Hovstad, K.A., 2018. Loss of semi-natural grassland in a boreal landscape: impacts of agricultural intensification and abandonment. J. Land Use Sci. 13, 375–390. <https://doi.org/10.1080/1747423X.2018.1539779>
- Azam, C., Kerbiriou, C., Vernet, A., Julien, J.-F., Bas, Y., Plichard, L., Maratrat, J., Le Viol, I., 2015. Is part-night lighting an effective measure to limit the impacts of artificial lighting on bats? Glob. Change Biol. 21, 4333–4341. <https://doi.org/10.1111/gcb.13036>
- Baessler, C., Klotz, S., 2006. Effects of changes in agricultural land-use on landscape structure and arable weed vegetation over the last 50 years. Agric. Ecosyst. Environ. 115, 43–50. <https://doi.org/10.1016/j.agee.2005.12.007>
- Baker, D., Barrett, S., Beale, C.M., Crawford, T.J., Ellis, S., Gullett, T., Mayhew, P.J., Parsons, M.S., Relf, P., Robertson, P., Small, J., Wainwright, D., 2016. Decline of a Rare Moth at Its Last Known English Site: Causes and Lessons for Conservation. PLoS One 11, e0157423. <https://doi.org/10.1371/journal.pone.0157423>

- Barlow, K.E., 1997. The diets of two phonic types of the bat *Pipistrellus pipistrellus* in Britain. *J. Zool.* 243, 597–609. <https://doi.org/10.1111/J.1469-7998.1997.TB02804.X>
- Barlow, K.E., Briggs, P.A., Haysom, K.A., Hutson, A.M., Lechiara, N.L., Racey, P.A., Walsh, A.L., Langton, S.D., 2015. Citizen science reveals trends in bat populations: The National Bat Monitoring Programme in Great Britain. *Biol. Conserv.* 182, 14–26. <https://doi.org/10.1016/j.biocon.2014.11.022>
- Batáry, P., Dicks, L.V., Kleijn, D., Sutherland, W.J., 2015. The role of agri-environment schemes in conservation and environmental management. *Conserv. Biol.* 29, 1006–1016. <https://doi.org/10.1111/cobi.12536>
- Bates, Douglas, Mächler, M., Bolker, B., Walker, S., 2015. Fitting Linear Mixed-Effects Models Using lme4. *J. Stat. Softw.* 67, 1–48. <https://doi.org/10.18637/jss.v067.i01>
- Baudry, J., Bunce, R.G.H., Burel, F., 2000. Hedgerows: An international perspective on their origin, function and management. *J. Environ. Manage.* 60, 7–22. <https://doi.org/10.1006/jema.2000.0358>
- Bayat, S., Geiser, F., Kristiansen, P., Wilson, S.C., 2014. Organic contaminants in bats: Trends and new issues. *Environ. Int.* 63, 40–52. <https://doi.org/10.1016/j.envint.2013.10.009>
- Bell, J.R., Blumgart, D., Shortall, C.R., 2020. Are insects declining and at what rate? An analysis of standardised, systematic catches of aphid and moth abundances across Great Britain. *Insect Conserv. Divers.* 13, 115–126. <https://doi.org/10.1111/icad.12412>
- Bellamy, C., Altringham, J., 2015. Predicting Species Distributions Using Record Centre Data: Multi-Scale Modelling of Habitat Suitability for Bat Roosts. *PLOS ONE* 10, e0128440. <https://doi.org/10.1371/journal.pone.0128440>
- Benmazouz, I., Jokimäki, J., Lengyel, S., Juhász, L., Kaisanlahti-Jokimäki, M.-L., Kardos, G., Paládi, P., Kövér, L., 2021. Corvids in Urban Environments: A Systematic Global Literature Review. *Animals* 11, 3226. <https://doi.org/10.3390/ani11113226>
- Berendse, F., Chamberlain, D., Kleijn, D., Schekkerman, H., 2004. Declining Biodiversity in Agricultural Landscapes and the Effectiveness of Agri-Environment Schemes. *Ambio* 33, 499–502.
- Berman, T.S., Ben-Ari, M., Henkin, Z., Inbar, M., 2018. Immediate and long-term facilitative effects of cattle grazing on a polyphagous caterpillar. <https://doi.org/10.1016/j.agee.2018.03.019>
- Biesmeijer, J.C., Roberts, S.P.M., Reemer, M., Ohlemüller, R., Edwards, M., Peeters, T., Schaffers, A.P., Potts, S.G., Kleukers, R., Thomas, C.D., Settele, J., Kunin, W.E., 2006. Parallel Declines in Pollinators and Insect-Pollinated Plants in Britain and the Netherlands. *Science* 313, 351–354. <https://doi.org/10.1126/science.1127863>
- Blary, C., Kerbiriou, C., Le Viol, I., Barré, K., 2021. Assessing the importance of field margins for bat species and communities in intensive agricultural landscapes. *Agric. Ecosyst. Environ.* 319, 107494. <https://doi.org/10.1016/j.agee.2021.107494>

- Boggard, A., 2004. Neolithic Farming in Central Europe : An Archaeobotanical Study of Crop Husbandry Practices. Taylor and Francis Group.
- Bolker, B., Brooks, M., Gardner, B., Lennert, C., Minami, M., n.d. Owls example: a zero-inflated, generalized linear mixed model for count data.
- Bork, E.W., Döbert, T.F., Grenke, J.S.J., Carlyle, C.N., Cahill, J.F., Boyce, M.S., 2021. Comparative Pasture Management on Canadian Cattle Ranches With and Without Adaptive Multipaddock Grazing. *Rangel. Ecol. Manag., Great Plains* 78, 5–14. <https://doi.org/10.1016/j.rama.2021.04.010>
- Börschig, C., Klein, A.-M., von Wehrden, H., Krauss, J., 2013. Traits of butterfly communities change from specialist to generalist characteristics with increasing land-use intensity. *Basic Appl. Ecol.* 14, 547–554. <https://doi.org/10.1016/j.baae.2013.09.002>
- Boughey, K.L., Lake, I.R., Haysom, K.A., Dolman, P.M., 2011. Improving the biodiversity benefits of hedgerows: How physical characteristics and the proximity of foraging habitat affect the use of linear features by bats. *Biol. Conserv.* 144, 1790–1798. <https://doi.org/10.1016/j.biocon.2011.02.017>
- Boutin, C., Baril, A., McCabe, S.K., Martin, P.A., Guy, M., 2011a. The Value of Woody Hedgerows for Moth Diversity on Organic and Conventional Farms. *Environ. Entomol.* 40, 560–569. <https://doi.org/10.1603/EN10105>
- Bouwman, H., Polder, A., Venter, B., Skaare, J.U., 2008. Organochlorine contaminants in cormorant, darter, egret, and ibis eggs from South Africa. *Chemosphere* 71, 227–241. <https://doi.org/10.1016/j.chemosphere.2007.09.057>
- Boyes, D.H., Evans, D.M., Fox, R., Parsons, M.S., Pocock, M.J.O., 2021. Street lighting has detrimental impacts on local insect populations. *Sci. Adv.* 7, eabi8322. <https://doi.org/10.1126/sciadv.abi8322>
- Brereton, T.M., Warren, M.S., Roy, D.B., Stewart, K., 2008. The changing status of the Chalkhill Blue butterfly *Polyommatus coridon* in the UK: the impacts of conservation policies and environmental factors. *J. Insect Conserv.* 12, 629–638. <https://doi.org/10.1007/s10841-007-9099-0>
- Broadbent, E.N., Asner, G.P., Keller, M., Knapp, D.E., Oliveira, P.J.C., Silva, J.N., 2008. Forest fragmentation and edge effects from deforestation and selective logging in the Brazilian Amazon. *Biol. Conserv.* 141, 1745–1757. <https://doi.org/10.1016/j.biocon.2008.04.024>
- Brodie, J.F., Williams, S., Garner, B., 2021. The decline of mammal functional and evolutionary diversity worldwide. *Proc. Natl. Acad. Sci.* 118, e1921849118. <https://doi.org/10.1073/pnas.1921849118>
- Brooks, A.C., Nopper, J., Weyers, A., Crosland, H., Foudoulakis, M., Haaf, S., Hackett, M., Lawrence, A., 2021. Assessing the Risks to Bats from Plant Protection Products: A Review of the Recent European Food Safety Authority Statement Regarding Toxicity and Exposure Routes. *Environ. Toxicol. Chem.* 40, 2978–2989. <https://doi.org/10.1002/etc.5209>
- Brooks, D.R., Bater, J.E., Clark, S.J., Monteith, D.T., Andrews, C., Corbett, S.J., Beaumont, D.A., Chapman, J.W., 2012b. Large carabid beetle declines in a United Kingdom monitoring network increases evidence for a

- widespread loss in insect biodiversity. *J. Appl. Ecol.* 49, 1009–1019.
<https://doi.org/10.1111/j.1365-2664.2012.02194.x>
- Brooks, M.E., Kristensen, K., Benthem, K.J. van, Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Mächler, M., Bolker, B.M., 2017. glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. *R J.* 9, 378–400.
- Browning, E., Barlow, K.E., Burns, F., Hawkins, C., Boughey, K., 2021. Drivers of European bat population change: a review reveals evidence gaps. *Mammal Rev.* 51, 353–368. <https://doi.org/10.1111/mam.12239>
- Buchanan, G.M., Grant, M.C., Sanderson, R.A., Pearce-Higgins, J.W., 2006. The contribution of invertebrate taxa to moorland bird diets and the potential implications of land-use management. *Ibis* 148, 615–628.
<https://doi.org/10.1111/j.1474-919X.2006.00578.x>
- Burgess, M.D., Bright, J.A., Morris, A.J., Field, R.H., Grice, P.V., Cooke, A.I., Peach, W., 2015. Influence of agri-environment scheme options on territory settlement by Yellowhammer (*Emberiza citronella*) and Corn Bunting (*Emberiza calandra*). *J. Ornithol.* 156, 153–163.
<https://doi.org/10.1007/s10336-014-1113-1>
- Burner, R.C., Selås, V., Kobro, S., Jacobsen, R.M., Sverdrup-Thygesen, A., 2021. Moth species richness and diversity decline in a 30-year time series in Norway, irrespective of species' latitudinal range extent and habitat. *J. Insect Conserv.* 25, 887–896. <https://doi.org/10.1007/s10841-021-00353-4>
- Burnham, K.P., Anderson, D.R. (Eds.), 2004. Model Selection and Multimodel Inference. Springer, New York, NY. <https://doi.org/10.1007/b97636>
- Burns, F., Eaton, M.A., Barlow, K.E., Beckmann, B.C., Brereton, T., Brooks, D.R., Brown, P.M.J., Al Fulaij, N., Gent, T., Henderson, I., Noble, D.G., Parsons, M., Powney, G.D., Roy, H.E., Stroh, P., Walker, K., Wilkinson, J.W., Wotton, S.R., Gregory, R.D., 2016. Agricultural Management and Climatic Change Are the Major Drivers of Biodiversity Change in the UK. *PLOS ONE* 11, e0151595.
<https://doi.org/10.1371/journal.pone.0151595>
- Burns, M., al Fulaij, N., Boersh-Supan, P.H., Boyd, R., J., Boswell, J., Bradfer-Lawrence, T., de Ornellas, P., de Palma, A., de Zylva, P., Dennis, E.B., 2023. State of Nature report 2023 | BTO [WWW Document]. URL <https://www.bto.org/our-work/science/publications/reports/state-of-nature/2023> (accessed 7.16.25).
- Buxton, M.N., Gaskett, A.C., Lord, J.M., Pattemore, D.E., 2022. A global review demonstrating the importance of nocturnal pollinators for crop plants. *J. Appl. Ecol.* 59, 2890–2901. <https://doi.org/10.1111/1365-2664.14284>
- Caro, G., Marrec, R., Gauffre, B., Roncoroni, M., Augiron, S., Bretagnolle, V., 2016. Multi-scale effects of agri-environment schemes on carabid beetles in intensive farmland. *Agric. Ecosyst. Environ.* 229, 48–56.
<https://doi.org/10.1016/j.agee.2016.05.009>

- Cel'uch, M., Kropil, R., 2008. Bats in a Carpathian beech-oak forest (Central Europe): habitat use, foraging assemblages and activity patterns. *Folia Zool.* 57, 358–372.
- Chaplin, S.P., Mills, J., Chiswell, H., 2021. Developing payment-by-results approaches for agri-environment schemes: Experience from an arable trial in England. *Land Use Policy* 109, 105698. <https://doi.org/10.1016/j.landusepol.2021.105698>
- Chu, A.C., Xu, R., 2024. From Neolithic Revolution to industrialization. *Macroecon. Dyn.* 28, 699–717. <https://doi.org/10.1017/S1365100523000214>
- Cipro, C.V.Z., Colabuono, F.I., Taniguchi, S., Montone, R.C., 2013. Persistent organic pollutants in bird, fish and invertebrate samples from King George Island, Antarctica. *Antarct. Sci.* 25, 545–552. <https://doi.org/10.1017/S0954102012001149>
- Cole, L.J., Pollock, M.L., Robertson, D., Holland, J.P., McCracken, D.I., Harrison, W., 2010. The influence of fine-scale habitat heterogeneity on invertebrate assemblage structure in upland semi-natural grassland. *Agric. Ecosyst. Environ.* 136, 69–80. <https://doi.org/10.1016/J.AGEE.2009.11.010>
- Collinge, S.K., Prudic, K.L., Oliver, J.C., 2003. Effects of Local Habitat Characteristics and Landscape Context on Grassland Butterfly Diversity. *Conserv. Biol.* 17, 178–187. <https://doi.org/10.1046/j.1523-1739.2003.01315.x>
- Concepción, E.D., Díaz, M., Kleijn, D., Andra's, A., Ldi, B., Bata'ry, B., Clough, Y., Gabriel, D., Herzog, F., Holzschuh, A., Knop, E., Jon, E., Marshall, P., Tscharncke, T., Verhulst, J., 2012. Interactive effects of landscape context constrain the effectiveness of local agri-environmental management. *J. Appl. Ecol.* 49, 695–705. <https://doi.org/10.1111/j.1365-2664.2012.02131.x>
- Cook, P.M., Tordoff, G.M., Davis, T.M., Parsons, M.S., Dennis, E.B., Fox, R., Botham, M.S., Bourn, N.A.D., 2022. Traits data for the butterflies and macro-moths of Great Britain and Ireland. *Ecology* 103. <https://doi.org/10.1002/ECY.3670>
- Cosyns, E., Claerbout, S., Lamoot, I., Hoffmann, M., 2005. Endozoochorous seed dispersal by cattle and horse in a spatially heterogeneous landscape. *Plant Ecol.* 178, 149–162. <https://doi.org/10.1007/s11258-004-2846-3>
- Cousins, S.A.O., Eriksson, O., 2008. After the hotspots are gone: Land use history and grassland plant species diversity in a strongly transformed agricultural landscape. *Appl. Veg. Sci.* 11, 365–374. <https://doi.org/10.3170/2008-7-18480>
- Cutter, J., Hovick, T., McGranahan, D., Harmon, J., Limb, R., Spiess, J., Geaumont, B., 2022. Cattle grazing results in greater floral resources and pollinators than sheep grazing in low-diversity grasslands. *Ecol. Evol.* 12, e8396. <https://doi.org/10.1002/ece3.8396>
- da Silva, H.M.S., Dubeux Jr, J.C.B., Silveira, M.L., dos Santos, M.V.F., de Freitas, E.V., de Almeida, B.G., 2019. Soil and Root Attributes in Pastures Managed under Different Stocking Rates and Nitrogen Fertilization Levels. *Agrosystems Geosci. Environ.* 2, 180031. <https://doi.org/10.2134/age2018.08.0031>

- Davidson-Watts, I., Jones, G., 2006a. Differences in foraging behaviour between *Pipistrellus pipistrellus* (Schreber, 1774) and *Pipistrellus pygmaeus* (Leach, 1825). *J. Zool.* 268, 55–62. <https://doi.org/10.1111/J.1469-7998.2005.00016.X>
- de Molina, M.G., García-Ruiz, R., Fernández, D.S., Casado, G.G., Cid, A., Amatea, J.I., 2015. Nutrient Balances and Management of Soil Fertility Prior to the Arrival of Chemical Fertilizers in Andalusia, Southern Spain. *Hum. Ecol. Rev.* 21, 23–48.
- De Smedt, P., Vangansbeke, P., Bracke, R., Schauwvlieghe, W., Willems, L., Mertens, J., Verheyen, K., 2019. Vertical stratification of moth communities in a deciduous forest in Belgium. *Insect Conserv. Divers.* 12, 121–130. <https://doi.org/10.1111/icad.12320>
- Deckers, B., Kerselaers, E., Gulinck, H., Muys, B., Hermy, M., 2005. Long-term spatio-temporal dynamics of a hedgerow network landscape in Flanders, Belgium. *Environ. Conserv.* 32, 20–29.
- Dennis, P., Young, M.R., Gordon, I.J., 1998. Distribution and abundance of small insects and arachnids in relation to structural heterogeneity of grazed, indigenous grasslands. *Ecol. Entomol.* 23, 253–264. <https://doi.org/10.1046/J.1365-2311.1998.00135.X>
- Dewally, K., Bark, R.H., Harwood, A.R., Lovett, A.A., 2025. Learning from the past and embracing future opportunities: Perceptions of new Environmental Land Management Schemes and private nature markets. *J. Rural Stud.* 119, 103723. <https://doi.org/10.1016/j.jrurstud.2025.103723>
- Dietz, M., Pir, J.B., Hillen, J., 2013. Does the survival of greater horseshoe bats and Geoffroy's bats in Western Europe depend on traditional cultural landscapes? *Biodivers. Conserv.* 22, 3007–3025. <https://doi.org/10.1007/s10531-013-0567-4>
- Domingo-Olivé, F., Bosch-Serra, À.D., Yagüe, M.R., Poch, R.M., Boixadera, J., 2016. Long term application of dairy cattle manure and pig slurry to winter cereals improves soil quality. *Nutr. Cycl. Agroecosystems* 104, 39–51. <https://doi.org/10.1007/s10705-015-9757-7>
- Downey, H., Aizlewood, S., Ash, A., Bavin, S., Burton, V., Chemais, M., Crawford, J., Gosling, R., Hewitt, D., Hugi, M., McHenry, E., Jackson, H., Nichols, C., Pyne, E., Reed-Beale, N., Underwood, F., Walsh, T., 2025. State of the UK's Woods and Trees 2025. Woodland Trust.
- Downs, N.C., Sanderson, L.J., 2010. Do Bats Forage Over Cattle Dung or Over Cattle? *Acta Chiropterologica* 12, 349–358. <https://doi.org/10.3161/150811010X537936>
- Dumont, B., Farruggia, A., Garel, J.-P., Bachelard, P., Boitier, E., Frain, M., 2009. How does grazing intensity influence the diversity of plants and insects in a species-rich upland grassland on basalt soils? *Grass Forage Sci.* 64, 92–105. <https://doi.org/10.1111/j.1365-2494.2008.00674.x>
- Dupont, Y.L., Strandberg, B., Damgaard, C., 2018. Effects of herbicide and nitrogen fertilizer on non-target plant reproduction and indirect effects

- on pollination in *Tanacetum vulgare* (Asteraceae). *Agric. Ecosyst. Environ.* 262, 76–82. <https://doi.org/10.1016/j.agee.2018.04.014>
- Edo, M., Entling, M.H., Herzog, F., Noe, K., Palma, J.H., Seithe, A., Simonson, W., Smith, J., Weiler, A., Rösch, V., 2025. Agroforestry systems favor bat conservation but only when old and grazed. *Glob. Ecol. Conserv.* 57, e03369. <https://doi.org/10.1016/j.gecco.2024.e03369>
- Edwards, C.B., Zipkin, E.F., Henry, E.H., Haddad, N.M., Forister, M.L., Burls, K.J., Campbell, S.P., Crone, E.E., Diffendorfer, J., Douglas, M.R., Drum, R.G., Fallon, C.E., Glassberg, J., Grames, E.M., Hatfield, R., Hershovich, S., Hoffman Black, S., Larsen, E.A., Leuenberger, W., Linders, M.J., Longcore, T., Marschalek, D.A., Michielini, J., Neupane, N., Ries, L., Shapiro, A.M., Swengel, A.B., Swengel, S.R., Taron, D.J., Van Deynze, B., Wiedmann, J., Thogmartin, W.E., Schultz, C.B., 2025. Rapid butterfly declines across the United States during the 21st century. *Science* 387, 1090–1094. <https://doi.org/10.1126/science.adp4671>
- Ekroos, J., Heliölä, J., Kuussaari, M., 2010. Homogenization of lepidopteran communities in intensively cultivated agricultural landscapes. *J. Appl. Ecol.* 47, 459–467.
- Elmiger, B.N., Finger, R., Ghazoul, J., Schaub, S., 2023. Biodiversity indicators for result-based agri-environmental schemes – Current state and future prospects. *Agric. Syst.* 204, 103538. <https://doi.org/10.1016/j.agsy.2022.103538>
- Emery, S.B., Franks, J.R., 2012. The potential for collaborative agri-environment schemes in England: Can a well-designed collaborative approach address farmers' concerns with current schemes? *J. Rural Stud.* 28, 218–231. <https://doi.org/10.1016/j.jrurstud.2012.02.004>
- Encarnação, J.A., Kierdorf, U., Wolters, V., 2006. Seasonal variation in nocturnal activity of male Daubenton's bats, *Myotis daubentonii* (Chiroptera: Vespertilionidae). *Folia Zool.* 55, 237–246.
- Eng, M.L., Stutchbury, B.J.M., Morrissey, C.A., 2019. A neonicotinoid insecticide reduces fueling and delays migration in songbirds. *Science* 365, 1177–1180. <https://doi.org/10.1126/science.aaw9419>
- Erdoğan, Ö., Karakaş, B., Yünlü, M.Z., 2025. The Trichoptera fauna of the Karpuz Stream and its relationships with water quality. *Biologia (Bratisl.)* 80, 641–653. <https://doi.org/10.1007/s11756-025-01870-2>
- Erhardt, A., 1985. Diurnal Lepidoptera: Sensitive Indicators of Cultivated and Abandoned Grassland. *J. Appl. Ecol.* 22, 849–861. <https://doi.org/10.2307/2403234>
- EUROBATS, 1991. Agreement on the Conservation of Bats in Europe.
- European Union, 2025. A look at European farms, Agricultural Census Results. Publications Office of the European Union.
- Evans, K.L., Wilson, J.D., Bradbury, R.B., 2007. Effects of crop type and aerial invertebrate abundance on foraging barn swallows *Hirundo rustica*. *Agric. Ecosyst. Environ.* 122, 267–273. <https://doi.org/10.1016/j.agee.2007.01.015>

- Ewert, S.P., Knörnschild, M., Jung, K., Frommolt, K.-H., 2023. Structurally rich dry grasslands – Potential stepping stones for bats in open farmland. *Front. Ecol. Evol.* 11. <https://doi.org/10.3389/fevo.2023.995133>
- Fartmann, T., 2006. Oviposition preferences, adjacency of old woodland and isolation explain the distribution of the Duke of Burgundy butterfly (*Hamearis lucina*) in calcareous grasslands in central Germany. *Ann. Zool. Fenn.* 43, 335–347.
- Farzana Khan Perveen, 2025. The Wonders of Diptera. IntechOpen.
- Felton, M., Jones, P., Tranter, R., Clark, J., Quaife, T., Lukac, M., 2023. Farmers' attitudes towards, and intentions to adopt, agroforestry on farms in lowland South-East and East England. *Land Use Policy* 131, 106668. <https://doi.org/10.1016/j.landusepol.2023.106668>
- Finch, D., Schofield, H., Mathews, F., 2020. Habitat Associations of Bats in an Agricultural Landscape: Linear Features Versus Open Habitats. *Animals* 10, 1856. <https://doi.org/10.3390/ani10101856>
- Földesi, R., Kovács-Hostyánszki, A., Körösi, Á., Somay, L., Elek, Z., Markó, V., Sárospataki, M., Bakos, R., Varga, Á., Nyisztor, K., Báldi, A., 2016. Relationships between wild bees, hoverflies and pollination success in apple orchards with different landscape contexts. *Agric. For. Entomol.* 18, 68–75. <https://doi.org/10.1111/afe.12135>
- Forister, M.L., Halsch, C.A., Nice, C.C., Fordyce, J.A., Dilts, T.E., Oliver, J.C., Prudic, K.L., Shapiro, A.M., Wilson, J.K., Glassberg, J., 2021. Fewer butterflies seen by community scientists across the warming and drying landscapes of the American West. *Science* 371, 1042–1045. <https://doi.org/10.1126/science.abe5585>
- Forman, R.T.T., Baudry, J., 1984. Hedgerows and hedgerow networks in landscape ecology. *Environ. Manage.* 8, 495–510. <https://doi.org/10.1007/BF01871575>
- Fox, R., 2013. The decline of moths in Great Britain: a review of possible causes. *Insect Conserv. Divers.* 6, 5–19. <https://doi.org/10.1111/j.1752-4598.2012.00186.x>
- Fox, R., Dennis, E.B., Harrower, C.A., Blumgart, D., Bell, J.R., Cook, P., Davis, A.M., Evans-Hill, L.J., Haynes, F., Isaac, N.J.B., Parsons, M.S., Pocock, M.J.O., Prescott, T., Randle, Z., Shortall, C.R., Tordoff, G.M., Tuson, D., Bourn, N.A.D., 2021. The State of Britain's Larger Moths 2021.
- Fox, R., Oliver, T.H., Harrower, C., Parsons, M.S., Thomas, C.D., Roy, D.B., 2014. Long-term changes to the frequency of occurrence of British moths are consistent with opposing and synergistic effects of climate and land-use changes. *J. Appl. Ecol.* 51, 949–957. <https://doi.org/10.1111/1365-2664.12256>
- Frafjord, K., 2021a. Activity patterns of the soprano pipistrelle *Pipistrellus pygmaeus* throughout the year in southern Norway. *BMC Zool.* 6, 1. <https://doi.org/10.1186/s40850-021-00065-x>
- Frafjord, K., 2021b. Activity patterns of the soprano pipistrelle *Pipistrellus pygmaeus* throughout the year in southern Norway. *BMC Zool.* 6, 1. <https://doi.org/10.1186/s40850-021-00065-x>

- Frank, C., Hertzog, L., Klimek, S., Schwieder, M., Tetteh, G.O., Böhner, H.G.S., Röder, N., Levers, C., Katzenberger, J., Kreft, H., Kamp, J., 2024. Woody semi-natural habitats modulate the effects of field size and functional crop diversity on farmland birds. *J. Appl. Ecol.* 61, 987–999. <https://doi.org/10.1111/1365-2664.14604>
- Fritsch, C., Appenzeller, B., Burkart, L., Coeurdassier, M., Scheifler, R., Raoul, F., Driget, V., Powolny, T., Gagnaison, C., Rieffel, D., Afonso, E., Goydadin, A.-C., Hardy, E.M., Palazzi, P., Schaeffer, C., Gaba, S., Bretagnolle, V., Bertrand, C., Pelosi, C., 2022. Pervasive exposure of wild small mammals to legacy and currently used pesticide mixtures in arable landscapes. *Sci. Rep.* 12, 15904. <https://doi.org/10.1038/s41598-022-19959-y>
- Froidevaux, Jérémy S.P., Boughey, K.L., Hawkins, C.L., Broyles, M., Jones, G., 2019. Managing hedgerows for nocturnal wildlife: Do bats and their insect prey benefit from targeted agri-environment schemes? *J. Appl. Ecol.* 56, 1610–1623. <https://doi.org/10.1111/1365-2664.13412>
- Froidevaux, Jérémy S. P., Broyles, M., Jones, G., 2019. Moth responses to sympathetic hedgerow management in temperate farmland. *Agric. Ecosyst. Environ.* 270–271, 55–64. <https://doi.org/10.1016/j.agee.2018.10.008>
- Froidevaux, J.S.P., Louboutin, B., Jones, G., 2017. Does organic farming enhance biodiversity in Mediterranean vineyards? A case study with bats and arachnids. *Agric. Ecosyst. Environ.* 249, 112–122. <https://doi.org/10.1016/j.agee.2017.08.012>
- Fuentes-Montemayor, E., Ferryman, M., Watts, K., Macgregor, N.A., Hambly, N., Brennan, S., Coxon, R., Langridge, H., Park, K.J., 2020. Small mammal responses to long-term large-scale woodland creation: the influence of local and landscape-level attributes. *Ecol. Appl.* 30, e02028. <https://doi.org/10.1002/eap.2028>
- Fuentes-Montemayor, E., Goulson, D., Cavin, L., Wallace, J.M., Park, K.J., 2013. Fragmented woodlands in agricultural landscapes: The influence of woodland character and landscape context on bats and their insect prey. *Agric. Ecosyst. Environ.* 172, 6–15. <https://doi.org/10.1016/j.agee.2013.03.019>
- Fuentes-Montemayor, E., Goulson, D., Cavin, L., Wallace, J.M., Park, K.J., 2012. Factors influencing moth assemblages in woodland fragments on farmland: Implications for woodland management and creation schemes. *Biol. Conserv.* 153, 265–275. <https://doi.org/10.1016/j.biocon.2012.04.019>
- Fuentes-Montemayor, E., Goulson, D., Park, K.J., 2011a. The effectiveness of agri-environment schemes for the conservation of farmland moths: Assessing the importance of a landscape-scale management approach. *J. Appl. Ecol.* 48, 532–542. <https://doi.org/10.1111/j.1365-2664.2010.01927.x>
- Fuentes-Montemayor, E., Goulson, D., Park, K.J., 2011b. Pipistrelle bats and their prey do not benefit from four widely applied agri-environment management prescriptions. *Biol. Conserv.* 144, 2233–2246. <https://doi.org/10.1016/j.biocon.2011.05.015>

- Fuentes-Montemayor, E., Watts, K., Sansum, P., Scott, W., Park, K.J., 2022. Moth community responses to woodland creation: The influence of woodland age, patch characteristics and landscape attributes. *Divers. Distrib.* 28, 1993–2007.
- Fuller, D.Q., Willcox, G., Allaby, R.G., 2011. Cultivation and domestication had multiple origins: arguments against the core area hypothesis for the origins of agriculture in the Near East. *World Archaeol.* 43, 628–652.
- Fuller, L., Fuentes-Montemayor, E., Watts, K., Macgregor, N.A., Bitenc, K., Park, K.J., 2018. Local-scale attributes determine the suitability of woodland creation sites for Diptera. *J. Appl. Ecol.* 55, 1173–1184.
- Fyfe, R.M., Woodbridge, J., Roberts, N., 2015. From forest to farmland: pollen-inferred land cover change across Europe using the pseudobiomization approach. *Glob. Change Biol.* 21, 1197–1212. <https://doi.org/10.1111/gcb.12776>
- Gagliardi, B., Pettigrove, V., 2013. Removal of intensive agriculture from the landscape improves aquatic ecosystem health. *Agric. Ecosyst. Environ.* 176, 1–8. <https://doi.org/10.1016/j.agee.2013.05.020>
- Gámez-Virués, S., Perović, D.J., Gossner, M.M., Börschig, C., Blüthgen, N., De Jong, H., Simons, N.K., Klein, A.-M., Krauss, J., Maier, G., Scherber, C., Steckel, J., Rothenwöhrer, C., Steffan-Dewenter, I., Weiner, C.N., Weisser, W., Werner, M., Tschardt, T., Westphal, C., 2015. Landscape simplification filters species traits and drives biotic homogenization. *Nat. Commun.* 6, 8568. <https://doi.org/10.1038/ncomms9568>
- Garrett, D.R., Pelletier, F., Garant, D., Bélisle, M., 2022a. Combined influence of food availability and agricultural intensification on a declining aerial insectivore. *Ecol. Monogr.* 92, e1518. <https://doi.org/10.1002/ecm.1518>
- Garrett, D.R., Pelletier, F., Garant, D., Bélisle, M., 2022b. Negative effects of agricultural intensification on the food provisioning rate of a declining aerial insectivore. *Ecosphere* 13, e4227. <https://doi.org/10.1002/ecs2.4227>
- Garrett, R., Ryschawy, J., Bell, L., Cortner, O., Ferreira, J., Garik, A.V., Gil, J., Klerkx, L., Moraine, M., Peterson, C., dos Reis, J.C., Valentim, J., 2020. Drivers of decoupling and recoupling of crop and livestock systems at farm and territorial scales. *Ecol. Soc.* 25. <https://doi.org/10.5751/ES-11412-250124>
- Gbèblonoudo Dassou, A., Laura Estelle Loko, Y., Toffa, J., Gbèmavo, C., Adjahossou, N., Tchakpa, C., Agboyi, L.K., Sanon, A., Dansi, A., Brévault, T., 2023. Within-field crop diversity and landscape complexity decrease the abundance of fall armyworm larvae in maize cropping systems. *Biol. Control* 183, 105260. <https://doi.org/10.1016/j.biocontrol.2023.105260>
- Geluso, K.N., Altenbach, J.S., Wilson, D.E., 1976. Bat Mortality: Pesticide Poisoning and Migratory Stress. *Science* 194, 184–186. <https://doi.org/10.1126/science.959845>
- Gilbert, M., Grégoire, J.-C., Freise, J.F., Heitland, W., 2004. Long-distance dispersal and human population density allow the prediction of invasive patterns in the horse chestnut leafminer *Cameraria ohridella*. *J. Anim. Ecol.* 73, 459–468. <https://doi.org/10.1111/j.0021-8790.2004.00820.x>

- Glendell, M., Vaughan, N., 2002. Foraging activity of bats in historic landscape parks in relation to habitat composition and park management. *Anim. Conserv.* 5, 309–316. <https://doi.org/10.1017/S1367943002004067>
- Goebel, K.M., Andersen, D.E., Rice, P.J., Davros, N.M., 2024. Effects of insecticide spray drift on arthropod prey resources of birds in grasslands in Minnesota. *J. Wildl. Manag.* 88, e22572. <https://doi.org/10.1002/jwmg.22572>
- Gordon, K., 2010. Mastering Mob Grazing. *Angus Journal*.
- Goulson, D., Nicholls, E., Botías, C., Rotheray, E.L., 2015. Bee declines driven by combined Stress from parasites, pesticides, and lack of flowers. *Science* 347. <https://doi.org/10.1126/science.1255957>
- Grabener, S., Oldeland, J., Shortall, C.R., Harrington, R., 2020. Changes in phenology and abundance of suction-trapped Diptera from a farmland site in the UK over four decades. *Ecol. Entomol.* 45, 1215–1219. <https://doi.org/10.1111/een.12873>
- Green, N.S., Wildhaber, M.L., Albers, J.L., Pettit, T.W., Hooper, M.J., 2024. Efficient mammal biodiversity surveys for ecological restoration monitoring. *Integr. Environ. Assess. Manag.* 20, 1969–1981. <https://doi.org/10.1002/ieam.4324>
- Grenke, J.S.J., Bork, E.W., Carlyle, C.N., Boyce, M.S., Cahill, J.F., 2022. Limited impacts of adaptive multi-paddock grazing systems on plant diversity in the Northern Great Plains. *J. Appl. Ecol.* 59, 1734–1744. <https://doi.org/10.1111/1365-2664.14181>
- Grevé, M.E., Marx, M.T., Eilmus, S., Ernst, M., Herrmann, J.D., Baden, C.U., Maus, C., 2024. Insect Decline—Evaluation of Potential Drivers of a Complex Phenomenon. *Insects* 15, 1021. <https://doi.org/10.3390/insects15121021>
- Griffin, D.R., Webster, F.A., Michael, C.R., 1960. The echolocation of flying insects by bats. *Anim. Behav.* 8, 141–154. [https://doi.org/10.1016/0003-3472\(60\)90022-1](https://doi.org/10.1016/0003-3472(60)90022-1)
- Gröebler, M.U., Korner-Nievergelt, F., von Hirschheydt, J., 2010. The reproductive benefits of livestock farming in barn swallows *Hirundo rustica*: quality of nest site or foraging habitat? *J. Appl. Ecol.* 47, 1340–1347.
- G. Rowse, E., Harris, S., Jones, G., 2018. Effects of dimming light-emitting diode street lights on light-opportunistic and light-averse bats in suburban habitats. *R. Soc. Open Sci.* 5. <https://doi.org/10.1098/rsos.180205>
- Gurr, G.M., Wratten, S.D., Luna, J.M., 2003. Multi-function agricultural biodiversity: pest management and other benefits. *Basic Appl. Ecol.* 4, 107–116. <https://doi.org/10.1078/1439-1791-00122>
- Hagemann, N., Gerling, C., Hölting, L., Kernecker, M., Markova-Nenova, N.N., Wätzold, F., Wendler, J., Cord, A.F., 2024. Improving result-based schemes for nature conservation in agricultural landscapes—challenges and best practices from selected European countries. *Reg. Environ. Change* 25, 12. <https://doi.org/10.1007/s10113-024-02324-2>
- Hale, J.D., Fairbrass, A.J., Matthews, T.J., Sadler, J.P., 2012. Habitat Composition and Connectivity Predicts Bat Presence and Activity at Foraging Sites in

- a Large UK Conurbation. PLOS ONE 7, e33300.
<https://doi.org/10.1371/journal.pone.0033300>
- Hallmann, C.A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., Stenmans, W., Müller, A., Sumser, H., Hörrén, T., Goulson, D., De Kroon, H., 2017a. More than 75 percent decline over 27 years in total flying insect biomass in protected areas. PLOS ONE 12, e0185809.
<https://doi.org/10.1371/journal.pone.0185809>
- Hamerow, H., Bogaard, A., Charles, M., Ramsey, C., Thomas, R., Forster, E., Holmes, M., McKerracher, M., Neil, S., Stroud, E., 2019. Feeding Anglo-Saxon England: the bioarchaeology of an agricultural revolution. *Antiquity* 93, e12. <https://doi.org/10.15184/aqy.2019.27>
- Hartig, F., 2024. DHARMA: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. R package version 0.4.7.
- Heim, O., Schröder, A., Eccard, J., Jung, K., Voigt, C.C., 2016. Seasonal activity patterns of European bats above intensively used farmland. *Agric. Ecosyst. Environ.* 233, 130–139. <https://doi.org/10.1016/j.agee.2016.09.002>
- Heim, O., Treitler, J.T., Tschapka, M., Knörnschild, M., Jung, K., 2015. The Importance of Landscape Elements for Bat Activity and Species Richness in Agricultural Areas. PLOS ONE 10, e0134443.
<https://doi.org/10.1371/journal.pone.0134443>
- Hesselbarth, M.H., Sciani, M., Wiegand, K., Nowosad, J., 2019. landscapemetrics: an open-source R tool to calculate landscape metrics. *Ecography* 42, 1648–1657. <https://doi.org/10.1111/ecog.04617>
- Hill, A.P., Prince, P., Snaddon, J.L., Doncaster, C.P., Rogers, A., 2019. AudioMoth: A low-cost acoustic device for monitoring biodiversity and the environment. *HardwareX* 6. <https://doi.org/10.1016/j.ohx.2019.e00073>
- Hillenbrand, M., Thompson, R., Wang, F., Apfelbaum, S., Teague, R., 2019. Impacts of holistic planned grazing with bison compared to continuous grazing with cattle in South Dakota shortgrass prairie. *Agric. Ecosyst. Environ.* 279, 156–168. <https://doi.org/10.1016/j.agee.2019.02.005>
- Hof, A.R., Bright, P.W., 2010. The value of agri-environment schemes for macro-invertebrate feeders: hedgehogs on arable farms in Britain. *Anim. Conserv.* 13, 467–473. <https://doi.org/10.1111/j.1469-1795.2010.00359.x>
- Holzschuh, A., Steffan-Dewenter, I., Kleijn, D., Tscharntke, T., 2007. Diversity of Flower-Visiting Bees in Cereal Fields: Effects of Farming System, Landscape Composition and Regional Context. *J. Appl. Ecol.* 44, 41–49.
- Hooda, P.S., Edwards, A.C., Anderson, H.A., Miller, A., 2000. A review of water quality concerns in livestock farming areas. *Sci. Total Environ.* 250, 143–167. [https://doi.org/10.1016/S0048-9697\(00\)00373-9](https://doi.org/10.1016/S0048-9697(00)00373-9)
- Howe, M.A., Hinde, D., Bennett, D., Palmer, S., 2004. The conservation of the belted beauty *Lycia zonaria britannica* (Lepidoptera, Geometridae) in the United Kingdom. *J. Insect Conserv.* 8, 159–166.
<https://doi.org/10.1007/s10841-004-1340-5>
- Humphreys, A.M., Govaerts, R., Ficinski, S.Z., Nic Lughadha, E., Vorontsova, M.S., 2019. Global dataset shows geography and life form predict modern

- plant extinction and rediscovery. *Nat. Ecol. Evol.* 3, 1043–1047.
<https://doi.org/10.1038/s41559-019-0906-2>
- HYDE, 2023. – with minor processing by Our World in Data. Land use: Cropland" [dataset].
- Inclán, D.J., Cerretti, P., Gabriel, D., Benton, T.G., Sait, S.M., Kunin, W.E., Gillespie, M.A.K., Marini, L., 2015. Organic farming enhances parasitoid diversity at the local and landscape scales. *J. Appl. Ecol.* 52, 1102–1109.
<https://doi.org/10.1111/1365-2664.12457>
- Infusino, M., Brehm, G., Marco, C., Scalercio, S., 2017. Assessing the efficiency of UV LEDs as light sources for sampling the diversity of macro-moths (Lepidoptera). *Eur. J. Entomol.* 114, 25–33.
<https://doi.org/10.14411/eje.2017.004>
- IPCC, 2023. Summary for Policymakers. In: Climate Change 2023: Synthesis Report. Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, H. Lee and J. Romero (eds.)]. IPCC, Geneva, Switzerland. <https://doi.org/10.59327/IPCC/AR6-9789291691647.001>
- IUCN, 2025. The IUCN Red List of Threatened Species.
- Jakusek, M., Brennensthul, M., Markowska, J., Wolski, K., Sobol, Ł., 2020. Effect of a Micronutrient Fertilizer and Fungicide on the Germination of Perennial Ryegrass Seeds (*Lolium perenne* L.) in Field Conditions. *Agronomy* 10, 1978. <https://doi.org/10.3390/agronomy10121978>
- Jaureguiberry, P., Titeux, N., Wiemers, M., Bowler, D.E., Coscieme, L., Golden, A.S., Guerra, C.A., Jacob, U., Takahashi, Y., Settele, J., Díaz, S., Molnár, Z., Purvis, A., 2022. The direct drivers of recent global anthropogenic biodiversity loss. *Sci. Adv.* 8, eabm9982. <https://doi.org/10.1126/sciadv.abm9982>
- Jayasinghe, S.L., Thomas, D.T., Anderson, J.P., Chen, C., Macdonald, B.C.T., 2023. Global Application of Regenerative Agriculture: A Review of Definitions and Assessment Approaches. *Sustainability* 15, 15941.
<https://doi.org/10.3390/su152215941>
- Jefferson, R.G., Smith, S.L.N., MacKintosh, E.J., 2019. Guidelines for the Selection of Biological SSSIs. Part 2: Detailed Guidelines for Habitats and Species Groups. Joint Nature Conservation Committee, Peterborough.
- Jenkins, E.V., Laine, T., Morgan, S.E., Cole, K.R., Speakman, J.R., 1998. Roost selection in the pipistrelle bat, *Pipistrellus pipistrellus* (Chiroptera: Vespertilionidae), in northeast Scotland. *Anim. Behav.* 56, 909–917.
<https://doi.org/10.1006/anbe.1998.0858>
- Jerrentrup, J.S., Wrage-Mönnig, N., Röver, K.-U., Isselstein, J., 2014. Grazing intensity affects insect diversity via sward structure and heterogeneity in a long-term experiment. *J. Appl. Ecol.* 51, 968–977.
- JNCC, 2019. Sixth National Report to the United Nations Convention on Biological Diversity: United Kingdom of Great Britain and Northern Ireland.
- Jochmann, R., Lipkow, E., Blanckenhorn, W.U., 2016. A field test of the effect of spiked ivermectin concentrations on the biodiversity of coprophagous

- dung insects in Switzerland. *Environ. Toxicol. Chem.* 35, 1947–1952. <https://doi.org/10.1002/etc.3081>
- Johnson, D.C., Teague, R., Apfelbaum, S., Thompson, R., Byck, P., 2022. Adaptive multi-paddock grazing management's influence on soil food web community structure for: increasing pasture forage production, soil organic carbon, and reducing soil respiration rates in southeastern USA ranches. *PeerJ* 10, e13750. <https://doi.org/10.7717/peerj.13750>
- Josefsson, J., Berg, Å., Hiron, M., Pärt, T., Eggers, S., 2013. Grass buffer strips benefit invertebrate and breeding skylark numbers in a heterogeneous agricultural landscape. *Agric. Ecosyst. Environ.* 181, 101–107. <https://doi.org/10.1016/j.agee.2013.09.018>
- Kameke, D., Kampen, H., Walther, D., 2017. Activity of *Culicoides* spp. (Diptera: Ceratopogonidae) inside and outside of livestock stables in late winter and spring. *Parasitol. Res.* 116, 881–889. <https://doi.org/10.1007/s00436-016-5361-2>
- Kapás, R.E., Plue, J., Kimberley, A., Cousins, S.A., Rozália Kapás, C.E., Török, P., Bullock, J.M., Jiménez-Alfaro, B., Sonkoly, J., 2020. Grazing livestock increases both vegetation and seed bank diversity in remnant and restored grasslands Funding information The Foundation for Baltic and East European Studies and Oscar and Lili Lamm Memorial Foundation. *J Veg Sci.* <https://doi.org/10.1111/jvs.12956>
- Kaukonen, M., Ruotsalainen, A.L., Wäli, P.R., Männistö, M.K., Setälä, H., Saravesi, K., Huusko, K., Markkola, A., 2013. Moth herbivory enhances resource turnover in subarctic mountain birch forests? *Ecol. Durh.* 94, 267–272. <https://doi.org/10.1890/12-0917.1>
- Kennedy, R., Fuentes-Montemayor, E., Park, K.J., Littlewood, N., 2026. Does mixed farming benefit moths? Exploring how different farming systems shape both local features and the wider landscape. *Agric. Ecosyst. Environ.* 396, 109996. <https://doi.org/10.1016/j.agee.2025.109996>
- Khan, M., Mohammad, A., Ahad, K., Katsoyiannis, A., Malik, S.A., Abdullaha, M., Rashid, A., Fasola, M., Hussain, A., Bokhari, H., Eqani, S.A.M.A.S., 2014. Cattle egrets as a biosentinels of persistent organic pollutants exposure. *Environ. Geochem. Health* 36, 375–384. <https://doi.org/10.1007/s10653-013-9556-5>
- Kheirodin, A., Cárcamo, H.A., Costamagna, A.C., 2020. Contrasting effects of host crops and crop diversity on the abundance and parasitism of a specialist herbivore in agricultural landscapes. *Landsc. Ecol.* 35, 1073–1087. <https://doi.org/10.1007/s10980-020-01000-0>
- Kilpatrick, J., Heywood, C., Smith, C., Wilson, L., Proter, C., Spink, J., 2008. Addressing the land use issues for non-food crops, in response to increasing fuel and energy generation opportunities.
- Kolkert, H.L., Smith, R., Rader, R., Reid, N., 2021. Prey removal in cotton crops next to woodland reveals periodic diurnal and nocturnal invertebrate predation gradients from the crop edge by birds and bats. *Sci. Rep.* 11, 5256. <https://doi.org/10.1038/s41598-021-84633-8>

- Kruess, A., Tscharntke, T., 2002. Contrasting responses of plant and insect diversity to variation in grazing intensity. *Biol. Conserv.* 106, 293–302. [https://doi.org/10.1016/S0006-3207\(01\)00255-5](https://doi.org/10.1016/S0006-3207(01)00255-5)
- Kühne, I., Arlettaz, R., Humbert, J.-Y., 2022. Landscape woody features, local management and vegetation composition shape moth communities in extensively managed grasslands. *Insect Conserv. Divers.* 15, 739–751. <https://doi.org/10.1111/icad.12600>
- Kurze, S., Heinken, T., Fartmann, T., 2018. Nitrogen enrichment in host plants increases the mortality of common Lepidoptera species. *Oecologia* 188, 1227–1237. <https://doi.org/10.1007/s00442-018-4266-4>
- Labuschagne, J., Agenbag, G.A., 2006. The effect of fertiliser N rates on growth of perennial ryegrass (*Lolium perenne*) and white clover (*Trifolium repens*) grown at high soil water levels under controlled conditions. *South Afr. J. Plant Soil* 23, 215–224. <https://doi.org/10.1080/02571862.2006.10634758>
- Lee, J.A., Gill, T.E., 2015. Multiple causes of wind erosion in the Dust Bowl. *Aeolian Res.* 19, 15–36. <https://doi.org/10.1016/j.aeolia.2015.09.002>
- Lefcheck, J.S., 2016. piecewiseSEM: Piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods Ecol. Evol.* 7, 573–579. <https://doi.org/10.1111/2041-210X.12512>
- Lemaire, G., Gastal, F., Franzluebbers, A., Chabbi, A., 2015. Grassland–Cropping Rotations: An Avenue for Agricultural Diversification to Reconcile High Production with Environmental Quality. *Environ. Manage.* 56, 1065–1077. <https://doi.org/10.1007/s00267-015-0561-6>
- Lentini, P.E., Gibbons, P., Fischer, J., Law, B., Hanspach, J., 2012. Bats in a Farming Landscape Benefit from Linear Remnants and Unimproved Pastures. *PLoS ONE* 7, 48201. <https://doi.org/10.1371/journal.pone.0048201>
- Leventon, J., Schaal, T., Velten, S., Dänhardt, J., Fischer, J., Abson, D.J., Newig, J., 2017. Collaboration or fragmentation? Biodiversity management through the common agricultural policy. *Land Use Policy* 64, 1–12. <https://doi.org/10.1016/j.landusepol.2017.02.009>
- Lindgren, J.P., Cousins, S.A.O., 2017. Island biogeography theory outweighs habitat amount hypothesis in predicting plant species richness in small grassland remnants. *Landsc. Ecol.* 32, 1895–1906. <https://doi.org/10.1007/s10980-017-0544-5>
- Lindsay, E.A., Cunningham, S.A., 2009. Livestock grazing exclusion and microhabitat variation affect invertebrates and litter decomposition rates in woodland remnants. *For. Ecol. Manag.* 258, 178–187. <https://doi.org/10.1016/j.foreco.2009.04.005>
- Lintott, P.R., Fuentes-Montemayor, E., Goulson, D., Park, K.J., 2014. Testing the effectiveness of surveying techniques in determining bat community composition within woodland. *Wildl. Res.* 40, 675–684. <https://doi.org/10.1071/WR13153>
- Litovska, I., van der Plas, F., Kleijn, D., 2025. Arthropod abundance is most strongly driven by crop and semi-natural habitat type rather than

- management in an intensive agricultural landscape in the Netherlands. *Agric. Ecosyst. Environ.* 378, 109298. <https://doi.org/10.1016/j.agee.2024.109298>
- Littlewood, N.A., 2008. Grazing impacts on moth diversity and abundance on a Scottish upland estate. *Insect Conserv. Divers.* 1, 151–160. <https://doi.org/10.1111/j.1752-4598.2008.00021.x>
- Liu, B., Yang, L., Yang, F., Wang, Q., Yang, Y., Lu, Y., Gardiner, M.M., 2016. Landscape diversity enhances parasitism of cotton bollworm (*Helicoverpa armigera*) eggs by *Trichogramma chilonis* in cotton. *Biol. Control* 93, 15–23. <https://doi.org/10.1016/j.biocontrol.2015.11.004>
- Liu, R.-L., van Kleunen, M., Pierce, S., Chytrý, M., Guo, K., Pyšek, P., Guo, W.-Y., 2025. Grime's CSR theory revisited: A whole-plant view of vascular plant functioning across contrasting environments. *J. Ecol.* n/a. <https://doi.org/10.1111/1365-2745.70146>
- Liu, Y., Axmacher, J.C., Li, L., Wang, C., Yu, Z., 2007. Ground beetle (Coleoptera: Carabidae) inventories: a comparison of light and pitfall trapping. *Bull. Entomol. Res.* 97, 577–583. <https://doi.org/10.1017/S0007485307005299>
- Losey, J.E., Vaughan, M., 2006. The Economic Value of Ecological Services Provided by Insects. *BioScience* 56, 311–323. [https://doi.org/10.1641/0006-3568\(2006\)56%255B311:TEVOES%255D2.O.CO;2](https://doi.org/10.1641/0006-3568(2006)56%255B311:TEVOES%255D2.O.CO;2)
- Love, B.E., Bork, E.W., Spaner, D., 2009. Tree seedling establishment in living fences: a low-cost agroforestry management practice for the tropics. *Agrofor. Syst.* 77, 1–8. <https://doi.org/10.1007/s10457-009-9244-8>
- Lučan, R.K., Hanák, V., Horáček, I., 2009. Long-term re-use of tree roosts by European forest bats. *For. Ecol. Manag.* 258, 1301–1306. <https://doi.org/10.1016/j.foreco.2009.06.032>
- Luke, S.H., Roy, H.E., Thomas, C.D., Tilley, L.A.N., Ward, S., Watt, A., Carnaghi, M., Jaworski, C.C., Tercel, M.P.T.G., Woodrow, C., Aown, S., Banfield-Zanin, J.A., Barnsley, S.L., Berger, I., Brown, M.J.F., Bull, J.C., Campbell, H., Carter, R.A.B., Charalambous, M., Cole, L.J., Ebejer, M.J., Farrow, R.A., Fartyal, R.S., Grace, M., Highet, F., Hill, J.K., Hood, A.S.C., Kent, E.S., Krell, F.-T., Leather, S.R., Leybourne, D.J., Littlewood, N.A., Lyons, A., Matthews, G., Mc Namara, L., Menéndez, R., Merrett, P., Mohammed, S., Murchie, A.K., Noble, M., Paiva, M.-R., Pannell, M.J., Phon, C.-K., Port, G., Powell, C., Rosell, S., Sconce, F., Shortall, C.R., Slade, E.M., Sutherland, J.P., Weir, J.C., Williams, C.D., Zielonka, N.B., Dicks, L.V., 2023. Grand challenges in entomology: Priorities for action in the coming decades. *Insect Conserv. Divers.* 16, 173–189. <https://doi.org/10.1111/icad.12637>
- Lye, G., Park, K., Osborne, J., Holland, J., Goulson, D., 2009. Assessing the value of Rural Stewardship schemes for providing foraging resources and nesting habitat for bumblebee queens (Hymenoptera: Apidae). <https://doi.org/10.1016/j.biocon.2009.03.032>

- Maas, B., Clough, Y., Tschardtke, T., 2013. Bats and birds increase crop yield in tropical agroforestry landscapes. *Ecol. Lett.* 16, 1480–1487.
<https://doi.org/10.1111/ele.12194>
- Macdonald, D.W., Tattersall, F.H., Service, K.M., Firbank, L.G., Feber, R.E., 2007. Mammals, agri-environment schemes and set-aside – what are the putative benefits? *Mammal Rev.* 37, 259–277.
https://doi.org/10.1046/J.1440-1770.2002.00172_37_4.X
- MacDonald, M.A., Angell, R., Dines, T.D., Dodd, S., Haysom, K.A., Hobson, R., Johnstone, I.G., Matthews, V., Morris, A.J., Parry, R., Shellswell, C.H., Skates, J., Tordoff, G.M., Wilberforce, E.M., 2019. Have Welsh agri-environment schemes delivered for focal species? Results from a comprehensive monitoring programme. *J. Appl. Ecol.* 56, 812–823.
- Macgregor, C.J., Scott-Brown, A.S., 2020. Nocturnal pollination: an overlooked ecosystem service vulnerable to environmental change. *Emerg. Top. Life Sci.* 4, 19–32. <https://doi.org/10.1042/etls20190134>
- MacLaren, C., Storkey, J., Strauss, J., Swanepoel, P., Dehnen-Schmutz, K., 2019. Livestock in diverse cropping systems improve weed management and sustain yields whilst reducing inputs. *J. Appl. Ecol.* 56, 144–156.
<https://doi.org/10.1111/1365-2664.13239>
- Madden, C.P., Suter, P.J., Nicholson, B.C., Austin, A.D., 1992. Deformities in chironomid larvae as indicators of pollution (pesticide) stress. *Netherland J. Aquat. Ecol.* 26, 551–557.
<https://doi.org/10.1007/BF02255289>
- Mammola, S., Pastorino, A., Debernardi, P., Patriarca, E., Garzoli, L., 2024. Long-term monitoring of a population of greater horseshoe bat emphasises the importance of a pest beetle prey on demographic trends. *Ecol. Evol.* 14, e70323. <https://doi.org/10.1002/ece3.70323>
- Mangels, J., Fiedler, K., Schneider, F.D., Blüthgen, N., 2017. Diversity and trait composition of moths respond to land-use intensification in grasslands: generalists replace specialists. *Biodivers. Conserv.* 26, 3385–3405.
<https://doi.org/10.1007/s10531-017-1411-z>
- Manning, P., Lewis, O.T., Beynon, S.A., 2018. Effects of the veterinary anthelmintic moxidectin on dung beetle survival and dung removal. *Entomol. Exp. Appl.* 166, 810–817. <https://doi.org/10.1111/eea.12730>
- Marston, C., Rowland, C.S., Morton, R.D., 2022. Land Cover Map 2021. 25m rasterised land parcels, GB.
- Martin, E.A., Seo, B., Park, C.-R., Reineking, B., Steffan-Dewenter, I., 2016. Scale-dependent effects of landscape composition and configuration on natural enemy diversity, crop herbivory, and yields. *Ecol. Appl.* 26, 448–462.
- Mathews, F., Harrower, C., 2020. IUCN – compliant Red List for Britain’s Terrestrial Mammals. Assessment by the mammal society under contract to Natural England, Natural Resources Wales and Scottish Natural Heritage.

- Mathews, F., Roche, N., Aughney, T., Jones, N., Day, J., Baker, J., Langton, S., 2015a. Barriers and benefits: implications of artificial night-lighting for the distribution of common bats in Britain and Ireland. *Philos. Trans. R. Soc. B Biol. Sci.* 370. <https://doi.org/10.1098/RSTB.2014.0124>
- Matthews, K., 2023. The Spatial Distribution of Stocking Rates Across Scotland.
- McCann, K.S., 2000. The diversity–stability debate. *Nature* 405, 228–33. <https://doi.org/10.1038/35012234>
- McCracken, G.F., Westbrook, J.K., Brown, V.A., Eldridge, M., Federico, P., Kunz, T.H., 2012. Bats Track and Exploit Changes in Insect Pest Populations. *PLOS ONE* 7, e43839. <https://doi.org/10.1371/journal.pone.0043839>
- McCracken, M.E., Woodcock, B.A., Lobley, M., Pywell, R.F., Saratsi, E., Swetnam, R.D., Mortimer, S.R., Harris, S.J., Winter, M., Hinsley, S., Bullock, J.M., 2015. Social and ecological drivers of success in agri–environment schemes: the roles of farmers and environmental context. *J. Appl. Ecol.* 52, 696–705.
- McKenzie, A.J., Emery, S.B., Franks, J.R., Whittingham, M.J., 2013. Landscape–scale conservation: collaborative agri–environment schemes could benefit both biodiversity and ecosystem services, but will farmers be willing to participate? *J. Appl. Ecol.* 50, 1274–1280.
- McMahon, B.J., Anderson, A., Carnus, T., Helden, A.J., Kelly–Quinn, M., Maki, A., Sheridan, H., Purvis, G., 2012. Different bioindicators measured at different spatial scales vary in their response to agricultural intensity. *Ecol. Indic.* 18, 676–683. <https://doi.org/10.1016/j.ecolind.2012.01.013>
- Meier, F., Grosche, L., Reusch, C., Runkel, V., van Schaik, J., Kerth, G., 2022. Long-term individualized monitoring of sympatric bat species reveals distinct species- and demographic differences in hibernation phenology. *BMC Ecol. Evol.* 22, 7. <https://doi.org/10.1186/s12862-022-01962-6>
- Mendenhall, C.D., Karp, D.S., Meyer, C.F.J., Hadly, E.A., Daily, G.C., 2014. Predicting biodiversity change and averting collapse in agricultural landscapes. *Nature* 509, 213–7. <https://doi.org/10.1038/nature13139>
- Merckx, T., Feber, R.E., Dulieu, R.L., Townsend, M.C., Parsons, M.S., Bourn, N.A.D., Riordan, P., Macdonald, D.W., 2009. Effect of field margins on moths depends on species mobility: Field-based evidence for landscape-scale conservation. *Agric. Ecosyst. Environ.* 129, 302–309. <https://doi.org/10.1016/j.agee.2008.10.004>
- Merckx, T., Feber, R.E., Mclaughlan, C., Bourn, N.A.D., Parsons, M.S., Townsend, M.C., Riordan, P., Macdonald, D.W., 2010. Shelter benefits less mobile moth species: The field-scale effect of hedgerow trees. *Agric. Ecosyst. Environ.* 138, 147–151. <https://doi.org/10.1016/j.agee.2010.04.010>
- Meunier, C., Martin, G., Barnaud, C., Ryschawy, J., 2024. Bucking the trend: Crop farmers’ motivations for reintegrating livestock. *Agric. Syst.* 214, 103820. <https://doi.org/10.1016/j.agsy.2023.103820>
- Millon, L., Julien, J.-F., Julliard, R., Kerbiriou, C., 2015. Bat activity in intensively farmed landscapes with wind turbines and offset measures. *Ecol. Eng.* 75, 250–257. <https://doi.org/10.1016/j.ecoleng.2014.11.050>

- Møller, A.P., 2019. Parallel declines in abundance of insects and insectivorous birds in Denmark over 22 years. *Ecol. Evol.* 9, 6581–6587. <https://doi.org/10.1002/ece3.5236>
- Monck-Whipp, L., Martin, A.E., Francis, C.M., Fahrig, L., 2017. Farmland heterogeneity benefits bats in agricultural landscapes. *Agri. Eco. Env.* <https://doi.org/10.1016/j.agee.2017.11.001>
- Moore, E., van Dijk, T., Asenga, A., Bongers, F., Sambalino, F., Veenendaal, E., Lohbeck, M., 2020. Species Selection and Management Under Farmer Managed Natural Regeneration in Dodoma, Tanzania. *Front. For. Glob. Change* 3. <https://doi.org/10.3389/ffgc.2020.563364>
- Mordue, S., Mill, A., Shirley, M., Aegerter, J., 2023. Foraging fidelity and individual specialisation in a temperate bat *Myotis nattereri*. *Eur. J. Wildl. Res.* 69, 121. <https://doi.org/10.1007/s10344-023-01744-5>
- Moschetti, M., Aurélien Besnard, , Couturier, T., Fonderflick, J., 2020. Grazing intensity negatively affects the maintenance of *Gentiana pneumonanthe* and the survival of *Phengaris alcon* egg-laying. *J. Insect Conserv.* 24, 343–351. <https://doi.org/10.1007/s10841-020-00220-8>
- Mosier, S., Apfelbaum, S., Byck, P., Calderon, F., Teague, R., Thompson, R., Cotrufo, M.F., 2021. Adaptive multi-paddock grazing enhances soil carbon and nitrogen stocks and stabilization through mineral association in southeastern U.S. grazing lands. *J. Environ. Manage.* 288, 112409. <https://doi.org/10.1016/j.jenvman.2021.112409>
- Mupepele, A.-C., Keller, M., Dormann, C.F., 2021. European agroforestry has no unequivocal effect on biodiversity: a time-cumulative meta-analysis. *BMC Ecol. Evol.* 21, 193. <https://doi.org/10.1186/s12862-021-01911-9>
- Musto, G.A., Swanepoel, P.A., Strauss, J.A., 2023. Regenerative agriculture v. conservation agriculture: potential effects on soil quality, crop productivity and whole-farm economics in Mediterranean-climate regions. *J. Agric. Sci.* 161, 328–338. <https://doi.org/10.1017/S0021859623000242>
- Mz, C., Lj, C., By, L., Jc, C., Yj, G., Q, Y., Tl, S., L, Y., Jy, Z., H, L., Xx, C., Aa, H., Sj, W., 2021. Migration trajectories of the diamondback moth *Plutella xylostella* in China inferred from population genomic variation. *Pest Manag. Sci.* 77. <https://doi.org/10.1002/ps.6188>
- Nagelkerke, N.J.D., 1991. A note on a general definition of the coefficient of determination. *Biometrika* 78, 691–692. <https://doi.org/10.1093/biomet/78.3.691>
- Nasu, Y., Murahama, S., Matsumuro, H., Ueda, K., Hirowatari, T., Yoshiyasu, Y., 2012. Relationships Between Nest-Dwelling Lepidoptera and Their Owl Hosts. *Ornithol. Sci.* 11, 77–85. <https://doi.org/10.2326/osj.11.77>
- National Statistics, 2023. The British Survey of Fertiliser Practice: Fertiliser use on farm crops for crop year 2022. National Statistics.
- Neu, C.W., Byers, C.R., Peek, J.M., 1974. A Technique for Analysis of Utilization-Availability Data. *J. Wildl. Manag.* 38, 541–545. <https://doi.org/10.2307/3800887>

- Neuweiler, G., 1989. Foraging ecology and audition in echolocating bats. *Trends Ecol. Evol.* 4, 160–166. [https://doi.org/10.1016/0169-5347\(89\)90120-1](https://doi.org/10.1016/0169-5347(89)90120-1)
- Nevens, F., Reheul, D., 2002. The nitrogen- and non-nitrogen-contribution effect of ploughed grass leys on the following arable forage crops: determination and optimum use. *Eur. J. Agron.* 16, 57–74. [https://doi.org/10.1016/S1161-0301\(01\)00115-0](https://doi.org/10.1016/S1161-0301(01)00115-0)
- NHBS, 2023. Wildlife and Survey Equipment, sweep net – heavy duty.
- Nicholls, B., Racey, P.A., 2006. Habitat Selection as a Mechanism of Resource Partitioning in Two Cryptic Bat Species *Pipistrellus pipistrellus* and *Pipistrellus pygmaeus*. *Ecography* 29, 697–708.
- Nicholls, B., Racey, P.A., 2006. Contrasting Home-Range Size and Spatial Partitioning in Cryptic and Sympatric *Pipistrellus* Bats. *Behav. Ecol. Sociobiol.* 61, 131–142.
- Noda, A., Yonesaka, R., Sasazaki, S., Mannen, H., 2018. The mtDNA haplogroup P of modern Asian cattle: A genetic legacy of Asian aurochs? *PLOS ONE* 13, e0190937. <https://doi.org/10.1371/journal.pone.0190937>
- Norberg, U.M., Rayner, J.M.V., Lighthill, M.J., 1997. Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 316, 335–427. <https://doi.org/10.1098/rstb.1987.0030>
- Nosal, P., Kowal, J., Węglarz, A., Wyrobisz-Papiewska, A., 2019. The occurrence and diversity of flies (Diptera) related to ruminant farming in southern Poland. *Ann. Parasitol.* 65. <https://doi.org/10.17420/ap6504.221>
- Öckinger, E., Eriksson, A.K., Smith, H.G., 2006. Effects of grassland abandonment, restoration and management on butterflies and vascular plants. *Biol. Conserv.* 133, 291–300. <https://doi.org/10.1016/j.biocon.2006.06.009>
- Olimpi *, E.M., Philpott, S.M., 2018. Agroecological farming practices promote bats. <https://doi.org/10.1016/j.agee.2018.06.008>
- Ongole, S., Sankaran, M., Karanth, K.K., 2018. Responses of aerial insectivorous bats to local and landscape-level features of coffee agroforestry systems in Western Ghats, India. *PLOS ONE* 13, e0201648. <https://doi.org/10.1371/journal.pone.0201648>
- Ordnance Survey GB, 2023. OS MasterMap® Topography Layer.
- Orłowski, G., Karg, J., 2013. Partitioning the effects of livestock farming on the diet of an aerial insectivorous passerine, the Barn Swallow *Hirundo rustica*. *Bird Study* 60, 111–123. <https://doi.org/10.1080/00063657.2012.748717>
- O'Rourke, K.H., 1997. The European Grain Invasion, 1870–1913. *J. Econ. Hist.* 57, 775–801. <https://doi.org/10.1017/S0022050700019537>
- O'Rourke, M.E., Rienzo-Stack, K., Power, A.G., 2011. A multi-scale, landscape approach to predicting insect populations in agroecosystems. *Ecol. Appl.* 21, 1782–1791.
- Outhwaite, C.L., McCann, P., Newbold, T., 2022. Agriculture and climate change are reshaping insect biodiversity worldwide. *Nature* 605, 97–102. <https://doi.org/10.1038/s41586-022-04644-x>

- Owens, A.C.S., Cochard, P., Durrant, J., Farnworth, B., Perkin, E.K., Seymoure, B., 2020. Light pollution is a driver of insect declines. *Biol. Conserv.* 241, 108259. <https://doi.org/10.1016/j.biocon.2019.108259>
- Pakeman, R.J., Fielding, D.A., Everts, L., Littlewood, N.A., 2019. Long-term impacts of changed grazing regimes on the vegetation of heterogeneous upland grasslands. *J. Appl. Ecol.* 56, 1794–1805. <https://doi.org/10.1111/1365-2664.13420>
- Paquette, S.R., Garant, D., Pelletier, F., Bélisle, M., 2013. Seasonal patterns in Tree Swallow prey (Diptera) abundance are affected by agricultural intensification. *Ecol. Appl.* 23, 122–133. <https://doi.org/10.1890/12-0068.1>
- Park, K.J., 2015. Mitigating the impacts of agriculture on biodiversity: bats and their potential role as bioindicators. *Mamm. Biol.* 80, 191–204. <https://doi.org/10.1016/J.MAMBIO.2014.10.004>
- Park, K.J., Jones, G., Ransome, R.D., 2000. Torpor, Arousal and Activity of Hibernating Greater Horseshoe Bats (*Rhinolophus ferrumequinum*). *Funct. Ecol.* 14, 580–588.
- Pelech, S., Hannon, S.J., 1995. Impact of Tent Caterpillar Defoliation on the Reproductive Success of Black-Capped Chickadees. *The Condor* 97, 1071–1074. <https://doi.org/10.2307/1369549>
- Perks, S.J., Goodenough, A.E., 2021. Comparing acoustic survey data for European bats: do walked transects or automated fixed-point surveys provide more robust data? *Wildl. Res.* 49, 314–323. <https://doi.org/10.1071/WR20123>
- Pimentel, N.T., da Rocha, P.A., Pedroso, M.A., Bernard, E., 2022. Estimates of insect consumption and guano input in bat caves in Brazil. *Mammal Res.* 67, 355–366. <https://doi.org/10.1007/s13364-022-00629-3>
- Pisa, L.W., Amaral-Rogers, V., Belzunces, L.P., Bonmatin, J.M., Downs, C.A., Goulson, D., Kreutzweiser, D.P., Krupke, C., Liess, M., McField, M., Morrissey, C.A., Noome, D.A., Settele, J., Simon-Delso, N., Stark, J.D., Van der Sluijs, J.P., Van Dyck, H., Wiemers, M., 2015a. Effects of neonicotinoids and fipronil on non-target invertebrates. *Environ. Sci. Pollut. Res.* 22, 68–102. <https://doi.org/10.1007/s11356-014-3471-x>
- Pocock, M.J.O., Jennings, N., 2008. Testing biotic indicator taxa: the sensitivity of insectivorous mammals and their prey to the intensification of lowland agriculture. *J. Appl. Ecol.* 45, 151–160. <https://doi.org/10.1111/j.1365-2664.2007.01361.x>
- Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O., Kunin, W.E., 2010. Global pollinator declines: trends, impacts and drivers. *Trends Ecol. Evol.* 25, 345–353. <https://doi.org/10.1016/j.tree.2010.01.007>
- Pöyry, J., Lindgren, S., Salminen, J., Kuussaari, M., 2004. Restoration of Butterfly and Moth Communities in Semi-Natural Grasslands by Cattle Grazing. *Ecol. Appl.* 14, 1656–1670. <https://doi.org/10.1890/03-5151>
- Pöyry, Juha, Luoto, Miska, Paukkunen, Juho, Pykälä, Juha, Raatikainen, Katja, Kuussaari, Mikko, Luoto, J., Raatikainen, J., Kuussaari, K., Pöyry, J., Luoto, M., Paukkunen, J., Pykälä, J., Raatikainen, K., Kuussaari, M., 2006. Different

responses of plants and herbivore insects to a gradient of vegetation height: an indicator of the vertebrate grazing intensity and successional age.

- Prinsloo, G.L., Uys, V.M., van Rooyen, M., 2015. Insects of Cultivated Plants and Natural Pastures in Southern Africa.
- Proença, V., Pereira, H.M., 2013. Comparing Extinction Rates: Past, Present, and Future, in: *Encyclopedia of Biodiversity*. Elsevier Inc., pp. 167–176. <https://doi.org/10.1016/B978-0-12-384719-5.00411-1>
- Puig-Montserrat, X., Flaquer, C., Gómez-Aguilera, N., Burgas, A., Mas, M., Tuneu, C., Marquès, E., López-Baucells, A., 2020. Bats actively prey on mosquitoes and other deleterious insects in rice paddies: Potential impact on human health and agriculture. *Pest Manag. Sci.* 76, 3759–3769. <https://doi.org/10.1002/ps.5925>
- Put, J.E., Fahrig, L., Mitchell, G.W., 2019. Bats respond negatively to increases in the amount and homogenization of agricultural land cover. *Landsc. Ecol.* 34, 1889–1903. <https://doi.org/10.1007/s10980-019-00855-2>
- QGIS Development Team, 2021. QGIS Geographic Information System. Open Source Geospatial Foundation Project.
- R Core Team, 2023a. R: A Language and Environment for Statistical Computing.
- Racey, P.A., 1973. The time of onset of hibernation in *Pipistrelle* bats, *Pipistrellus pipistrellus*. *J. Zool.* 171, 465–467. <https://doi.org/10.1111/j.1469-7998.1973.tb02225.x>
- Raderschall, C.A., Bommarco, R., Lindström, S.A.M., Lundin, O., 2021. Landscape crop diversity and semi-natural habitat affect crop pollinators, pollination benefit and yield. *Agric. Ecosyst. Environ.* 306, 107189. <https://doi.org/10.1016/j.agee.2020.107189>
- Rákosy, L., Schmitt, T., 2011. Are butterflies and moths suitable ecological indicator systems for restoration measures of semi-natural calcareous grassland habitats? *Ecol. Indic.* 11, 1040–1045. <https://doi.org/10.1016/j.ecolind.2010.10.010>
- Rapiya, M., Hawkins, H.-J., Muchenje, V., Mupangwa, J.F., Marufu, M.C., Dzama, K., Mapiye, C., 2019. Rotational grazing approaches reduces external and internal parasite loads in cattle. *Afr. J. Range Forage Sci.* 36, 151–159. <https://doi.org/10.2989/10220119.2019.1628104>
- Rasmussen, S.L., Pertoldi, C., Roslev, P., Vorkamp, K., Nielsen, J.L., 2024. A Review of the Occurrence of Metals and Xenobiotics in European Hedgehogs (*Erinaceus europaeus*). *Animals* 14, 232. <https://doi.org/10.3390/ani14020232>
- Redlich, S., Martin, E.A., Steffan-Dewenter, I., 2018. Landscape-level crop diversity benefits biological pest control. *J. Appl. Ecol.* 55, 2419–2428. <https://doi.org/10.1111/1365-2664.13126/FORMAT/PDF>
- Regan, J.T., Marton, S., Barrantes, O., Ruane, E., Hanegraaf, M., Berland, J., Korevaar, H., Pellerin, S., Nesme, T., 2017. Does the recoupling of dairy and crop production via cooperation between farms generate environmental

- benefits? A case-study approach in Europe. *Eur. J. Agron.* 82, 342–356.
<https://doi.org/10.1016/J.EJA.2016.08.005>
- Rehberger, E., West, P.C., Spillane, C., McKeown, P.C., 2023. What climate and environmental benefits of regenerative agriculture practices? an evidence review. *Environ. Res. Commun.* 5, 052001.
<https://doi.org/10.1088/2515-7620/acd6dc>
- Reif, J., Hanzelka, J., 2020. Continent-wide gradients in open-habitat insectivorous bird declines track spatial patterns in agricultural intensity across Europe. *Glob. Ecol. Biogeogr.* 29, 1988–2013.
<https://doi.org/10.1111/geb.13170>
- Reppert, S.M., de Roode, J.C., 2018. Demystifying Monarch Butterfly Migration. *Curr. Biol.* 28, R1009–R1022. <https://doi.org/10.1016/j.cub.2018.02.067>
- Ridding, L.E., Redhead, J.W., Pywell, R.F., 2015. Fate of semi-natural grassland in England between 1960 and 2013: A test of national conservation policy. *Glob. Ecol. Conserv.* 4, 516–525.
<https://doi.org/10.1016/j.gecco.2015.10.004>
- Ridley, G., Parrish, T., Chantry, T., Richmond, A., MacArthur, R., Garthwaite, D., 2022. Pesticide Usage Survey Report 309: Arable Crops in the United Kingdom. National Statistics.
- Rigot, T., Vercauteren Drubbel, M., Delécolle, J.-C., Gilbert, M., 2013. Farms, pastures and woodlands: the fine-scale distribution of Palearctic *Culicoides* spp. biting midges along an agro-ecological gradient. *Med. Vet. Entomol.* 27, 29–38. <https://doi.org/10.1111/j.1365-2915.2012.01032.x>
- Robinson, R.A., Sutherland, W.J., 2002. Post-war changes in arable farming and biodiversity in Great Britain. *J. Appl. Ecol.* 39, 157–176.
<https://doi.org/10.1046/j.1365-2664.2002.00695.x>
- Rosch, V., Hafner, G., Reiff, J.M., Entling, M., 2023. Increase in breeding bird abundance and diversity with semi-natural habitat in vineyard landscapes. *PLoS One* 18.
<https://doi.org/DOI:10.1371/journal.pone.0284254>
- Rudel, T.K., Kwon, O.J., Paul, B.K., Boval, M., Rao, I.M., Burbano, D., McGroddy, M., Lerner, A.M., White, D., Cuchillo, M., Luna, M., Peters, M., 2016. Do smallholder, mixed crop-livestock livelihoods encourage sustainable agricultural practices? A meta-analysis. *Land* 5.
<https://doi.org/10.3390/land5010006>
- Runhaar, H., Polman, N., 2018. Partnering for nature conservation: NGO-farmer collaboration for meadow bird protection in the Netherlands. *Land Use Policy* 73, 11–19. <https://doi.org/10.1016/j.landusepol.2018.01.033>
- Russ, J.M., Briffa, M., Montgomery, W.I., 2003a. Seasonal patterns in activity and habitat use by bats (*Pipistrellus* spp. and *Nyctalus leisleri*) in Northern Ireland, determined using a driven transect. *J. Zool.* 259, 289–299.
<https://doi.org/10.1017/S0952836902003254>
- Russ, J.M., Montgomery, W.I., 2002. Habitat associations of bats in Northern Ireland: implications for conservation. *Biol. Conserv.* 108, 49–58.
[https://doi.org/10.1016/S0006-3207\(02\)00089-7](https://doi.org/10.1016/S0006-3207(02)00089-7)

- Russo, D., Salinas-Ramos, V.B., Cistrone, L., Smeraldo, S., Bosso, L., Ancillotto, L., 2021. Do We Need to Use Bats as Bioindicators? *Biology* 10, 693. <https://doi.org/10.3390/biology10080693>
- Russo, L., Ruedenauer, F., Gronert, A., Van De Vreken, I., Vanderplanck, M., Michez, D., Klein, A., Leonhardt, S., Stout, J.C., 2023. Fertilizer and herbicide alter nectar and pollen quality with consequences for pollinator floral choices. *PeerJ* 11, e15452. <https://doi.org/10.7717/peerj.15452>
- Rydell, J., Nyman, S., Eklöf, J., Jones, G., Russo, D., 2017. Testing the performances of automated identification of bat echolocation calls: A request for prudence. *Ecol. Indic.* 78, 416–420. <https://doi.org/10.1016/j.ecolind.2017.03.023>
- Ryschawy, J., Choisis, N., Choisis, J.P., Joannon, A., Gibon, A., 2012a. Mixed crop–livestock systems: an economic and environmental-friendly way of farming? *animal* 6, 1722–1730. <https://doi.org/10.1017/S1751731112000675>
- Sabanov, A., Soteras, R., Hajdas, I., Naumov, G., Antolín, F., 2024. New research on crop diversity of the early farmers in southeastern Europe (ca. 6400 – 5700 bce). *Veg. Hist. Archaeobotany* 33, 63–74. <https://doi.org/10.1007/s00334-023-00940-2>
- SAC Consulting, 2024a. The Farm Management Handbook, The UK reference for farm business management.
- Salvati, L., Zitti, M., Perini, L., 2016. Fifty Years on: Long-term Patterns of Land Sensitivity to Desertification in Italy. *Land Degrad. Dev.* 27, 97–107. <https://doi.org/10.1002/ldr.2226>
- Sanderson, L.J., 2016. Do Bats Forage Over Cattle Dung or Over Cattle? <https://doi.org/10.3161/150811010X537936>
- Sands, B., Machado, M.R., White, A., Zent, E., Gould, R., 2023. Moving towards an anti-colonial definition for regenerative agriculture. *Agric. Hum. Values* 40, 1697–1716. <https://doi.org/10.1007/s10460-023-10429-3>
- Santorufio, L., Ienco, A., Scalercio, S., 2021. Climate warming drives divergence of montane butterfly communities in Southern Italy. *Reg. Environ. Change* 21, 56. <https://doi.org/10.1007/s10113-021-01782-2>
- Saunders, W.C., Fausch, K.D., 2007. Improved Grazing Management Increases Terrestrial Invertebrate Inputs that Feed Trout in Wyoming Rangeland Streams. *Trans. Am. Fish. Soc.* 136, 1216–1230. <https://doi.org/10.1577/T06-260.1>
- Scheffczyk, A., Floate, K.D., Blanckenhorn, W.U., Düring, R.-A., Klockner, A., Lahr, J., Lumaret, J.-P., Salamon, J.-A., Tixier, T., Wohde, M., Römbke, J., 2016. Nontarget effects of ivermectin residues on earthworms and springtails dwelling beneath dung of treated cattle in four countries. *Environ. Toxicol. Chem.* 35, 1959–1969. <https://doi.org/10.1002/etc.3306>
- Schlegel, A.J., Assefa, Y., Bond, H.D., Wetter, S.M., Stone, L.R., 2015. Corn Response to Long-Term Applications of Cattle Manure, Swine Effluent, and Inorganic Nitrogen Fertilizer. *Agron. J.* 107, 1701–1710. <https://doi.org/10.2134/agronj14.0632>

- Schmid, R.B., Welch, K.D., Lundgren, J.G., 2024a. A Survey of the Dung-Dwelling Arthropod Community in the Pastures of the Northern Plains. *Insects* 15, 38. <https://doi.org/10.3390/insects15010038>
- Schmid, R.B., Welch, K.D., Teague, R., Lundgren, J.G., 2024b. Adaptive Multipaddock (AMP) Pasture Management Increases Arthropod Community Guild Diversity Without Increasing Pests. *Rangel. Ecol. Manag.* 94, 141–148. <https://doi.org/10.1016/j.rama.2024.03.001>
- Schmidt, M.H., Tscharntke, T., 2005. Landscape Context of Sheetweb Spider (Araneae: Linyphiidae) Abundance in Cereal Fields. *J. Biogeogr.* 32, 467–473.
- Schmitz, A., Isselstein, J., 2020. Effect of grazing system on grassland plant species richness and vegetation characteristics: Comparing horse and cattle grazing. *Sustain. Switz.* 12. <https://doi.org/10.3390/SU12083300>
- Schmitz, J., Hahn, M., Brühl, C.A., 2014. Agrochemicals in field margins – An experimental field study to assess the impacts of pesticides and fertilizers on a natural plant community. *Agric. Ecosyst. Environ.* 193, 60–69. <https://doi.org/10.1016/j.agee.2014.04.025>
- Schmitz, M.F., Sánchez, I.A., de Aranzabal, I., 2007. Influence of management regimes of adjacent land uses on the woody plant richness of hedgerows in Spanish cultural landscapes. *Biol. Conserv.* 135, 542–554. <https://doi.org/10.1016/j.biocon.2006.10.053>
- Schuster, M.Z., Pelissari, A., de Moraes, A., Harrison, S.K., Sulc, R.M., Lustosa, S.B.C., Anghinoni, I., Carvalho, P.C.F., 2016. Grazing intensities affect weed seedling emergence and the seed bank in an integrated crop–livestock system. *Agric. Ecosyst. Environ.* 232, 232–239. <https://doi.org/10.1016/J.AGEE.2016.08.005>
- Scottish Government, 2023. Rural Payments and Services, Management or Restoration of Hedgerows.
- Scottish Government, 2009. Chapter 3: The Diversity of Scottish Soils, in: The Scottish Soils Framework.
- Senawi, J., Kingston, T., 2019. Clutter negotiating ability in an ensemble of forest interior bats is driven by body mass. *J. Exp. Biol.* 222, jeb203950. <https://doi.org/10.1242/jeb.203950>
- Shaw, H., 1995. How Many Bison Originally Populated Western Rangelands?
- Shennan-Farpón, Y., Vion-Loisel, A., van Soesbergen, A., López-Gunn, E., García Asenjo, C., van Delden, H., Douglas, C., Mulligan, M., 2025. Understanding regenerative agriculture in Europe: An analysis of academic literature, stakeholder perceptions and policy comparing Spain and the UK. *Environ. Sci. Policy* 172, 104172. <https://doi.org/10.1016/j.envsci.2025.104172>
- Shiba, T., Sugawara, K., 2010. Inhibitory effect of an endophytic fungus, *Neotyphodium lolii*, on the feeding and survival of *Ostrinia furnacalis* (Guenee) (Lepidoptera: Pyralidae) and *Sesamia inferens* (Walker) (Lepidoptera: Noctuidae) on infected *Lolium perenne*. *Appl. Entomol. Zool.* 45, 225–231. <https://doi.org/10.1303/aez.2010.225>

- Shipley, B., 2000a. A New Inferential Test for Path Models Based on Directed Acyclic Graphs. *Struct. Equ. Model. Multidiscip. J.* 7, 206–218.
https://doi.org/10.1207/S15328007SEM0702_4
- Shirey, V., Neupane, N., Guralnick, R., Ries, L., 2024. Rising minimum temperatures contribute to 50 years of occupancy decline among cold-adapted Arctic and boreal butterflies in North America. *Glob. Change Biol.* 30, e17205. <https://doi.org/10.1111/gcb.17205>
- Shortall, C.R., Moore, A., Smith, E., Hall, M.J., Woiwod, I.P., Harrington, R., 2009. Long-term changes in the abundance of flying insects. *Insect Conserv. Divers.* 2, 251–260. <https://doi.org/10.1111/j.1752-4598.2009.00062.x>
- Sierra-Durán, C., Torres-Alcántara, Á., López-Baucells, A., Medellín, R.A., 2025. Bats over rice: Assessing the contribution of insectivorous bats to pest suppression in Mexican rice fields. *Agric. Ecosyst. Environ.* 383, 109503. <https://doi.org/10.1016/j.agee.2025.109503>
- Simmons, N.B., Ciranello, A.L., 2025. Bat Species of the World: A taxonomic and geographic database.
- Smith, O.M., Kennedy, C.M., Owen, J.P., Northfield, T.D., Latimer, C.E., Snyder, W.E., 2020. Highly diversified crop?livestock farming systems reshape wild bird communities. *Ecol. Appl.* 30, 1–14.
- Soil Survey of Scotland Staff, 1981. Soil maps of Scotland at a scale of 1:250 000.
- Souther, S., Loeser, M., Crews, T.E., Sisk, T., 2020. Drought exacerbates negative consequences of high-intensity cattle grazing in a semiarid grassland. *Ecol. Appl.* 30, e02048. <https://doi.org/10.1002/eap.2048>
- Sow, A., Seye, D., Faye, E., Benoit, L., Galan, M., Haran, J., Brévault, T., 2020. Birds and bats contribute to natural regulation of the millet head miner in tree-crop agroforestry systems. *Crop Prot.* 132, 105127. <https://doi.org/10.1016/j.cropro.2020.105127>
- Stahlschmidt, P., Brühl, C.A., 2012a. Bats as bioindicators – the need of a standardized method for acoustic bat activity surveys. *Methods Ecol. Evol.* 3, 503–508. <https://doi.org/10.1111/j.2041-210X.2012.00188.x>
- Starik, N., Göttert, T., Heitlinger, E., Zeller, U., 2019. Bat Community Responses to Structural Habitat Complexity Resulting from Management Practices Within Different Land Use Types — A Case Study from North-Eastern Germany. *Acta Chiropterologica* 20, 387–405. <https://doi.org/10.3161/15081109ACC2018.20.2.010>
- Stebbing, R.E., Griffith, F., 1986. Distribution and status of bats in Europe. Institute of Terrestrial Ecology, Abbots Ripton, Huntingdon, Cambs.
- Sterling, P., Henwood, B., 2020. Field Guide to the Caterpillars of Great Britain and Ireland. Bloomsbury Wildlife Guides.
- Sterling, P., Parsons, M., 2018. Field Guide to the Micro moths of Great Britain and Ireland. Bloomsbury Wildlife Guides.
- Stork, N.E., 2018. How Many Species of Insects and Other Terrestrial Arthropods Are There on Earth? *Annu. Rev. Entomol.* 63, 31–45. <https://doi.org/10.1146/annurev-ento-020117-043348>

- Svenningsen, C.S., Peters, B., Bowler, D.E., Dunn, R.R., Bonn, A., Tøttrup, A.P., 2024. Insect biomass shows a stronger decrease than species richness along urban gradients. *Insect Conserv. Divers.* 17, 182–188. <https://doi.org/10.1111/icad.12694>
- Swift, S.M., Racey, P.A., Avery, M.I., 1985. Feeding Ecology of *Pipistrellus pipistrellus* (Chiroptera: Vespertilionidae) During Pregnancy and Lactation. II. Diet. *Source J. Anim. Ecol.* 54, 217–225.
- Sylvester, K., Cunfer, G., 2008. An Unremembered Diversity: Mixed Husbandry and the American Grasslands. *Agricultural history* 83, 352–383.
- Tanno, K., Willcox, G., 2006. How Fast Was Wild Wheat Domesticated? *Science* 311, 1886–1886.
- Tassoni, S., Becker, D., Kasten, M.K., Morinière, J., Grass, I., 2024. Insect conservation in agricultural landscapes needs both high crop heterogeneity and semi-natural habitats. *Glob. Ecol. Conserv.* 55, e03218. <https://doi.org/10.1016/j.gecco.2024.e03218>
- Teets, K.D., Loeb, S.C., Jachowski, D.S., 2019. Detection probability of bats using active versus passive monitoring. *Acta Chiropterologica* 21, 205–213. <https://doi.org/10.3161/15081109ACC2019.21.1.017>
- Teutscherová, N., Vázquez, E., Sotelo, M., Villegas, D., Velásquez, N., Baquero, D., Pulleman, M., Arango, J., 2021. Intensive short-duration rotational grazing is associated with improved soil quality within one year after establishment in Colombia. *Appl. Soil Ecol.* 159, 103835. <https://doi.org/10.1016/j.apsoil.2020.103835>
- The British Ecological Society, 2025. Regenerative Agriculture in the UK: An Ecological Perspective.
- The Yorck Project, 2002. 10.000 Meisterwerke der Malerei.
- Thomas, H.S., 2012. Ranchers Sing the Praises of Mob Grazing Cattle.
- Thomas, S.R., Noordhuis, R., Holland, J.M., Goulson, D., 2002. Botanical diversity of beetle banks: Effects of age and comparison with conventional arable field margins in southern UK. *Agric. Ecosyst. Environ.* 93, 403–412. [https://doi.org/10.1016/S0167-8809\(01\)00342-5](https://doi.org/10.1016/S0167-8809(01)00342-5)
- Thorbek, P., Bilde, T., 2004. Reduced Numbers of Generalist Arthropod Predators after Crop Management. *J. Appl. Ecol.* 41, 526–538.
- Tilman, D., Isbell, F., Cowles, J.M., 2014. Biodiversity and Ecosystem Functioning. *Annu. Rev. Ecol. Evol. Syst.* 45, 471–493.
- Tracy, B.F., Bauer, R.B., 2019. Evaluating mob stocking for beef cattle in a temperate grassland. *PLOS ONE* 14, e0226360. <https://doi.org/10.1371/journal.pone.0226360>
- Trickett, T., Warner, D.J., 2022. Earthworm Abundance Increased by Mob-Grazing Zero-Tilled Arable Land in South-East England. *Earth* 3, 895–906. <https://doi.org/10.3390/earth3030052>
- Tscharntke, T., Grass, I., Wanger, T.C., Westphal, C., Batáry, P., 2021. Beyond organic farming – harnessing biodiversity-friendly landscapes. *Trends Ecol. Evol.* 36, 919–930. <https://doi.org/10.1016/j.tree.2021.06.010>

- Tuneu-Corral, C., Puig-Montserrat, X., Flaquer, C., Mata, V.A., Rebelo, H., Cabeza, M., López-Baucells, A., 2024. Bats and rice: Quantifying the role of insectivorous bats as agricultural pest suppressors in rice fields. *Ecosyst. Serv.* 66, 101603. <https://doi.org/10.1016/j.ecoser.2024.101603>
- Tyler, T., 2020. Relationship between moth (night active Lepidoptera) diversity and vegetation characteristics in southern Sweden. *J. Insect Conserv.* 24, 1005–1015. <https://doi.org/10.1007/s10841-020-00270-y>
- Uhl, B., Wölfling, M., Fiedler, K., 2021. Qualitative and Quantitative Loss of Habitat at Different Spatial Scales Affects Functional Moth Diversity. *Front. Ecol. Evol.* 9. <https://doi.org/10.3389/fevo.2021.637371>
- UK Government, 2024. Farming evidence – key statistics. UK Government. <https://www.gov.uk/government/publications/farming-evidence-pack-a-high-level-overview-of-the-uk-agricultural-industry/farming-evidence-key-statistics-accessible-version>
- UK Government, 2025. Organic farming statistics 2024: United Kingdom. UK Government.
- UK Government, 2021. Convert Livestock Numbers into Livestock Units.
- Unwin, D.M., 1981. Key to the families of british Diptera.
- Vaiglova, P., Bogaard, A., Collins, M., Cavanagh, W., Mee, C., Renard, J., Lamb, A., Gardeisen, A., Fraser, R., 2014. An integrated stable isotope study of plants and animals from Kouphovouno, southern Greece: a new look at Neolithic farming. *J. Archaeol. Sci.* 42, 201–215. <https://doi.org/10.1016/j.jas.2013.10.023>
- Valdespino, C., Sosa, V.J., 2017. Effect of landscape tree cover, sex and season on the bioaccumulation of persistent organochlorine pesticides in fruit bats of riparian corridors in eastern Mexico. *Chemosphere* 175, 373–382. <https://doi.org/10.1016/j.chemosphere.2017.02.071>
- Valtonen, A., Hirka, A., Szocs, L., Ayres, M.P., Roininen, H., Csoka, G., 2017. Long-term species loss and homogenization of moth communities in Central Europe. *J. Anim. Ecol.* 86, 730–738. <https://doi.org/doi:%252010.1111/1365-2656.12687>
- Van der Meij, T., Van Strien, A.J., Haysom, K.A., Dekker, J., Russ, J., Biala, K., Bihari, Z., Jansen, E., Langton, S., Kurali, A., Limpens, H., Meschede, A., Petersons, G., Presetnik, P., Prüger, J., Reiter, G., Rodrigues, L., Schorcht, W., Uhrin, M., Vintulis, V., 2015. Return of the bats? A prototype indicator of trends in European bat populations in underground hibernacula. *Mamm. Biol.*, Special Issue: Bats as Bioindicators 80, 170–177. <https://doi.org/10.1016/j.mambio.2014.09.004>
- Van Der Sluis, T., Arts, B., Kok, K., Bogers, M., Busck, A.G., Sepp, K., Loupa-Ramos, I., Pavlis, V., Geamana, N., Crouzat, E., 2019. Drivers of European landscape change: stakeholders' perspectives through Fuzzy Cognitive Mapping. *Landsc. Res.* 44, 458–476. <https://doi.org/10.1080/01426397.2018.1446074>
- Van Dobben, H.F., Quik, C., Wamelink, G.W.W., Lantinga, E.A., 2019. Vegetation composition of *Lolium perenne*-dominated grasslands under organic

- and conventional farming. *Basic Appl. Ecol.* 36, 45–53.
<https://doi.org/10.1016/j.baae.2019.03.002>
- van Noordwijk, C.G.E., Flierman, D.E., Remke, E., WallisDeVries, M.F., Berg, M.P., 2012. Impact of grazing management on hibernating caterpillars of the butterfly *Melitaea cinxia* in calcareous grasslands. *J. Insect Conserv.* 16, 909–920. <https://doi.org/10.1007/s10841-012-9478-z>
- van Zanten, B.T., Verburg, P.H., Espinosa, M., Gomez-y-Paloma, S., Galimberti, G., Kantelhardt, J., Kapfer, M., Lefebvre, M., Manrique, R., Piorr, A., Raggi, M., Schaller, L., Targetti, S., Zasada, I., Viaggi, D., 2014. European agricultural landscapes, common agricultural policy and ecosystem services: a review. *Agron. Sustain. Dev.* 34, 309–325. <https://doi.org/10.1007/s13593-013-0183-4>
- Venables, W.N., Ripely, B.D., 2002. *Modern Applied Statistics with S*, 4th ed. Springer New York.
- Venturi, M., Piras, F., Corrieri, F., Martinez Aguilar, E.A., Santoro, A., 2022. The multifunctional role of linear features in traditional silvopastoral systems: the sabana de morro in Dolores (El Salvador) and the pastures with carob trees in Ragusa (Italy). *Biodivers. Conserv.* 31, 2315–2327. <https://doi.org/10.1007/s10531-021-02220-9>
- Vesterinen, E.J., Puisto, A.I.E., Blomberg, A.S., Lilley, T.M., 2018. Table for five, please: Dietary partitioning in boreal bats. *Ecol. Evol.* 8, 10914–10937. <https://doi.org/10.1002/ECE3.4559/FORMAT/PDF>
- Vesterinen, E.J., Ruokolainen, L., Wahlberg, N., Peña, C., Roslin, T., Laine, V.N., Vasko, V., Sääksjärvi, I.E., Norrdahl, K., Lilley, T.M., 2016. What you need is what you eat? Prey selection by the bat *Myotis daubentonii*. *Mol. Ecol.* 25, 1581–1594. <https://doi.org/10.1111/mec.13564>
- Vicari, M., Hatcher, P.E., Ayres, P.G., 2002. Combined Effect of Foliar and Mycorrhizal Endophytes on an Insect Herbivore. *Ecology* 83, 2452–2464. [https://doi.org/10.1890/0012-9658\(2002\)083%255B2452:CEOFAM%255D2.O.CO;2](https://doi.org/10.1890/0012-9658(2002)083%255B2452:CEOFAM%255D2.O.CO;2)
- Vickery, J. a., Tallwin, J. r., Feber, R. e., Asteraki, E. j., Atkinson, P. w., Fuller, R. j., Brown, V. k., 2001. The management of lowland neutral grasslands in Britain: effects of agricultural practices on birds and their food resources. *J. Appl. Ecol.* 38, 647–664. <https://doi.org/10.1046/j.1365-2664.2001.00626.x>
- Wagner, D.L., 2019. Insect Declines in the Anthropocene.
- Wagner, D.L., Fox, R., Salcido, D.M., Dyer, L.A., 2021. A window to the world of global insect declines: Moth biodiversity trends are complex and heterogeneous 118, 2002549117. <https://doi.org/10.1073/pnas.2002549117/-/DCSupplemental>
- Wagner, M., Waterton, C., Norton, L.R., 2023. Mob grazing: A nature-based solution for British farms producing pasture-fed livestock. *Nat.-Based Solut.* 3, 100054. <https://doi.org/10.1016/j.nbsj.2023.100054>
- Walsh, A.L., Harris, S., 1996a. Foraging Habitat Preferences of Vespertilionid Bats in Britain. *J. Appl. Ecol.* 33, 508–518. <https://doi.org/10.2307/2404980>

- Walsh, A.L., Harris, S., 1996b. Factors Determining the Abundance of Vespertilionid Bats in Britain: Geographical, Land Class and Local Habitat Relationships. *J. Appl. Ecol.* 33, 519–529. <https://doi.org/10.2307/2404981>
- Walters, C.L., Freeman, R., Collen, A., Dietz, C., Brock Fenton, M., Jones, G., Obrist, M.K., Puechmaille, S.J., Sattler, T., Siemers, B.M., Parsons, S., Jones, K.E., 2012. A continental-scale tool for acoustic identification of European bats. *J. Appl. Ecol.* 49, 1064–1074. <https://doi.org/10.1111/j.1365-2664.2012.02182.x>
- Walton, R.E., Sayer, C.D., Bennion, H., Axmacher, J.C., 2020. Nocturnal pollinators strongly contribute to pollen transport of wild flowers in an agricultural landscape. *Biol. Lett.* 16, 20190877. <https://doi.org/10.1098/rsbl.2019.0877>
- Waring, P., Townsend, M., 2018. Field Guide to the Moths of Great Britain and Ireland, Bloomsbury Wildlife Guides. Bloomsbury publishing.
- Waringer, J.A., 2003. Light-Trapping of Caddisflies at the Thaya (Lower Austria), a River Influenced by Pulsating Hypolimnetic Water Release. *Int. Rev. Hydrobiol.* 88, 139–153. <https://doi.org/10.1002/iroh.200390010>
- Welti, E.A.R., Zajicek, P., Frenzel, M., Ayasse, M., Bornholdt, T., Buse, J., Classen, A., Dziock, F., Engelmann, R.A., Englmeier, J., Fellendorf, M., Förschler, M.I., Fricke, U., Ganuza, C., Hippke, M., Hoenselaar, G., Kaus-Thiel, A., Kerner, J., Kilian, D., Mandery, K., Marten, A., Monaghan, M.T., Morkel, C., Müller, J., Puffpaff, S., Redlich, S., Richter, R., Rojas-Botero, S., Scharnweber, T., Scheiffarth, G., Yáñez, P.S., Schumann, R., Seibold, S., Steffan-Dewenter, I., Stoll, S., Tobisch, C., Twietmeyer, S., Uhler, J., Vogt, J., Weis, D., Weisser, W.W., Wilmking, M., Haase, P., 2022. Temperature drives variation in flying insect biomass across a German malaise trap network. *Insect Conserv. Divers.* 15, 168–180. <https://doi.org/10.1111/icad.12555>
- Wickramasinghe, L.P., Harris, S., Jones, G., Jennings, N.V., 2004. Abundance and species richness of nocturnal insects on organic and conventional farms: Effects of agricultural intensification on bat foraging. *Conserv. Biol.* 18, 1283–1292. <https://doi.org/10.1111/J.1523-1739.2004.00152.X/FORMAT/PDF>
- Wilby, A., Thomas, M.B., 2002. Natural enemy diversity and pest control: patterns of pest emergence with agricultural intensification. *Ecol. Lett.* 5, 353–360. <https://doi.org/10.1046/j.1461-0248.2002.00331.x>
- Wildlife Acoustic Inc, 2024. Kaleidoscope.
- Wildlife Acoustics, 2011. Echo Meter User Manual.
- Willis, R., 2020. A Guide to Mob Grazing Livestock. *Farmer's Weekly*.
- Windsor, F.M., Pereira, M.G., Tyler, C.R., Ormerod, S.J., 2019. River organisms as indicators of the distribution and sources of persistent organic pollutants in contrasting catchments. *Environ. Pollut.* 255, 113144. <https://doi.org/10.1016/j.envpol.2019.113144>
- Work, T.T., McCullough, D.G., Cavey, J.F., Komsa, R., 2005. Arrival rate of nonindigenous insect species into the United States through foreign trade. *Biol. Invasions* 7, 323–332. <https://doi.org/10.1007/s10530-004-1663-x>

- Wuepper, D., Wiebecke, I., Meier, L., Vogelsanger, S., Bramato, S., Fürholz, A., Finger, R., 2024. Agri-environmental policies from 1960 to 2022. *Nat. Food* 5, 323–331. <https://doi.org/10.1038/s43016-024-00945-8>
- Xu, W., Xu, Y., Han, Z., Yao, J., Tryjanowski, P., Wang, H., 2025. Disentangling the relative effects of semi-natural habitats within different landscape agricultural intensities on bird communities. *Avian Res.* 16, 100228. <https://doi.org/10.1016/j.avrs.2025.100228>
- Ye, S., Cao, P., Lu, C., 2024. Annual time-series 1 km maps of crop area and types in the conterminous US (CropAT-US): cropping diversity changes during 1850–2021. *Earth Syst. Sci. Data* 16, 3453–3470. <https://doi.org/10.5194/essd-16-3453-2024>
- Zani, C.F., Gowing, J., Abbott, G.D., Taylor, J.A., Lopez-Capel, E., Cooper, J., 2021. Grazed temporary grass-clover leys in crop rotations can have a positive impact on soil quality under both conventional and organic agricultural systems. *Eur. J. Soil Sci.* 72, 1513–1529. <https://doi.org/10.1111/EJSS.13002>
- Zayed, Y., Loft, P., 2019. Agriculture: historical statistics, Briefing paper. Common library.
- Zeder, M.A., Hesse, B., 2000. The Initial Domestication of Goats (*Capra hircus*) in the Zagros Mountains 10,000 Years Ago. *Science* 287, 2254–2257. <https://doi.org/10.1126/science.287.5461.2254>
- Zhang, H., You, C.-M., Wang, J.-Y., Woodcock, B.A., Chen, Y.-J., Ji, X.-Y., Wan, N.-F., 2024. A parasitic wasp-releasing engineering to promote ecosystem services in paddy systems. *Agric. Ecosyst. Environ.* 373, 109126. <https://doi.org/10.1016/j.agee.2024.109126>
- Zhao, G., Yang, F., Li, J., Xing, H., Ren, F., Pang, G., Li, Y., 2020. Toxicities of Neonicotinoid-Containing Pesticide Mixtures on Nontarget Organisms. *Environ. Toxicol. Chem.* 39, 1884–1893. <https://doi.org/10.1002/etc.4842>
- Zhao, Z.-H., Hui, C., Hardev, S., Ouyang, F., Dong, Z., Ge, F., 2014. Responses of Cereal Aphids and Their Parasitic Wasps to Landscape Complexity. *J. Econ. Entomol.* 107, 630–637. <https://doi.org/10.1603/EC13054>
- Zhou, S., Long, H., Xing, H., Zhang, K., Wang, R., Zhang, E., 2023. Human activities facilitated the decline of forest ecosystem in East Asia after 5000 a BP. *Earth-Sci. Rev.* 245, 104552. <https://doi.org/10.1016/j.earscirev.2023.104552>
- Zucca, C., Fleiner, R., Bonaiuti, E., Kang, U., 2022. Land degradation drivers of anthropogenic sand and dust storms. *CATENA* 219, 106575. <https://doi.org/10.1016/j.catena.2022.106575>
- Ockinger, E., Smith, H.G., 2007. Semi-Natural Grasslands as Population Sources for Pollinating Insects in Agricultural Landscapes. *J. Appl. Ecol.* 44, 50–59.