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

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ABSTRACT

Moths 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. We investigate 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. Woodland edge density, which was higher on mixed farms, increased micro moth abundance and species richness. 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, highlighting the need for more research to find livestock management practices that are beneficial for moths.

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 2500 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

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reducing the abundance and diversity of plant food available in field margins (Dupont et al., 2018). Alarmingly, 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 host plant 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; Kruess and Tscharntke, 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; Fig. 1).

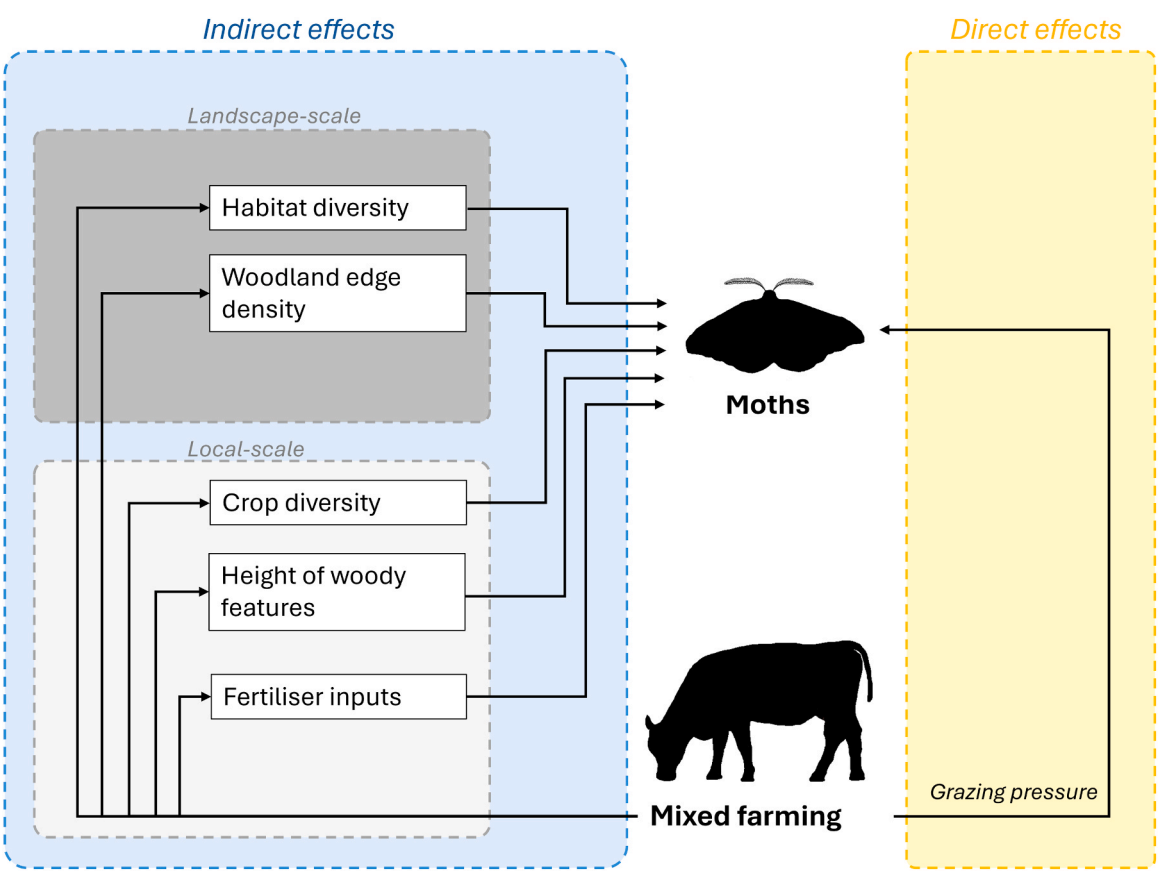

Fig. 1. Conceptual model showing potential pathways through which mixed farming could influence both local (light grey box) and landscape (dark grey box) features with indirect impacts (blue box) on moths, as well as a potential direct pathway (yellow box) between mixed farming and moths.

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. We 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?

2. Method

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. 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 20 km 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; Fig. 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 100 m distance between traps to reduce interference (Truxa and Fiedler, 2012).

Moth traps were collected within 1.5 h 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. We differentiated between macro (larger moths) and micro (smaller moths) according to classification by Waring and Townsend (2018) and Sterling et al. (2018). Macro moths were identified to species using Waring and Townsend (2018). Micro moths were identified to species level where possible using Sterling et al. (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 where 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).

2.3. Landscape analysis

QGIS version 3.28.1 (QGIS Development Team, 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 et al., 2022) 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 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.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

Fig. 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).

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 1000 m 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.) 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.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.

2.4. 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 15 m 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 our study site, we 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.4.

2.5. Statistical analysis

All statistical analysis was carried out in R version 4.3.2.

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. We 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 our variables of interest (farm type and crop diversity; Fig. 3). High landcover diversity is known to benefit moths (Ekroos et al., 2010) and was included in our SEMs at a scale of 1000 m, as this was found to be most relevant to moths in our 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. We measured 'woody feature' both in terms of feature height and feature type. However, woody features classified as 'hedgerows' were significantly lower in height that those classified as 'treelines' or 'woodland patches' (Anova $p < 0.0001$), so we included the continuous variable of woody feature height in SEMs. Temperature was also included as a predictor variable to account for changes in moth

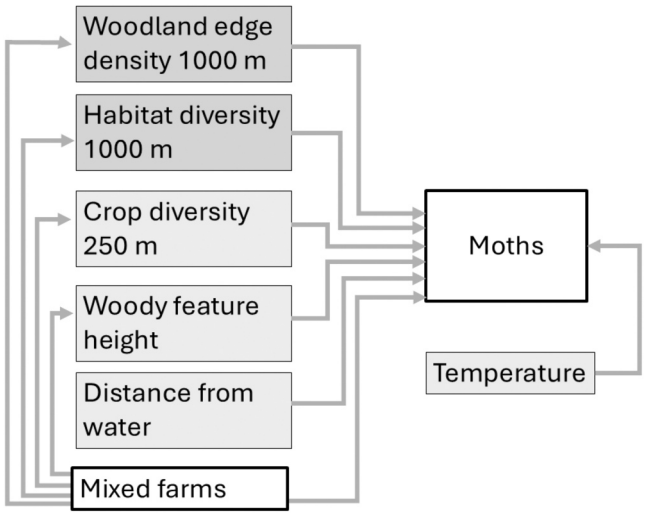

Fig. 3. Metamodel showing all variables and pathways that were included in our SEMs. Dark grey boxes indicate landscape-scale variables whilst light grey boxes indicate local-scale attributes.

emergence numbers throughout the season (Jonason et al., 2013). As there were multiple moth traps per farm, we 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)). We 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. 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. 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.5.). Validity of models was confirmed by ensuring that the Fisher's C statistic was not significant ($P > 0.05$).

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 %). We 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).

2.5.3. *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 we summed moth catches from crop-crop margins for each farm to obtain a farm-level moth community. Although we 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 et al., 2022). 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.

3. Results

Across all traps ($n = 110$) a total of 6801 individual macro-moths and 2680 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 (Fig. 4.a.). Similarly, 59 % of all macro moth species and 56 % of all micro moth species were farmland species (Fig. 4.b.).

3.1. Direct and indirect effect of farm type on moths

3.1.1. Landscape composition

Farming type had a marginally non-significant effect ($0.1 > P > 0.05$) on woodland edge density within a 1000 m 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 (Fig. 5). An increase of just over 22 m (1 standard deviation) of woodland edge per hectare increased mean micro moth abundance by 27 % (SE ± 12 %) and mean species richness by 19 % (± 7 %). This also held true for farmland micro moth abundance with an increase of 28 % (± 12 %), but not for farmland micro moth species richness or diversity, where the relationship was non-significant (Fig. 5 & Figure S.1.). Macro moths were unaffected by changes in woodland edge density. Habitat diversity at the 1000 m 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 ($P = 0.07$).

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 % (± 7 %). The combined direct and indirect effects of mixed farming in this model led to an overall negative effect for micro moth species richness (Fig. 5). Farm type did not influence any other local or landscape-scale variables included in these models.

3.2. 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 8 m in height increased mean farmland micro moth abundance by 18 % (± 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 (Fig. 5). Distance from water only affected macro moths, with abundance, species richness and diversity decreasing with increasing distance from freshwater (Figure S.1.). The random effect of 'Farm' also explained some of the variation in moths in all models.

3.3. 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 (Fig. 6.), margin type had no significant effect on the abundance, richness or diversity of any of the moth groups.

3.4. Moth community composition

3.4.1. Influence of landscape-scale features on community composition

NMDS plots showed no visible clustering of moth communities by farm type (Fig. 7.a, 7.b). 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 (Fig. 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.8, $P = 0.04$), with no visible clustering of woody plant-feeding species in areas of greater woodland edge density (Figure S.2). There was no significant effect of woodland edge density on macro moth community composition (Fig. 7.a).

3.4.2. Influence of local-scale features on community composition

At the local scale (trap-level), moth community composition was unaffected by field margin type (Fig. 7.c,d), 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 (Fig. 7.c, d). 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

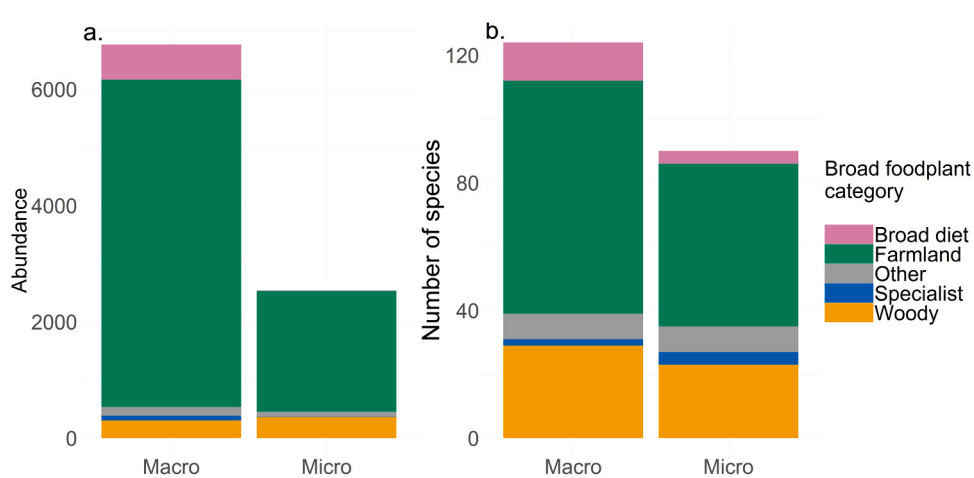

Fig. 4. Abundance of macro and micro moths by functional group (a) and total number of macro and micro moth species included in each guild (b).

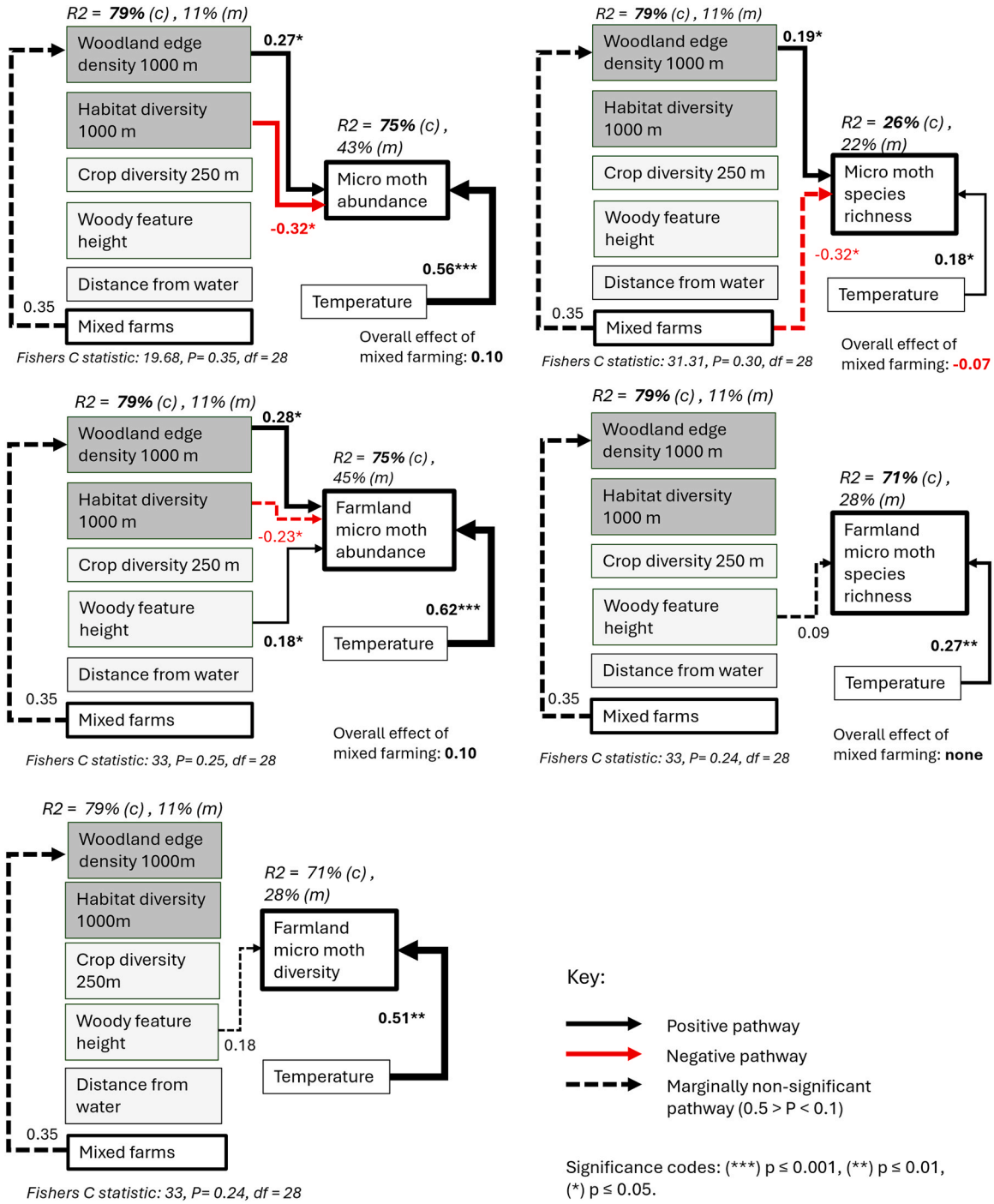

Fig. 5. Path diagrams for all SEMs where variables of interest had a significant effect on moths. Non-significant models are provided in Fig. S1 and model summaries for all SEMs are provided in table S.5. Boxes represent variables included in each model. Standard estimates for each significant pathway 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: (***) $p \leq 0.001$, (**) $p \leq 0.01$, (*) $p \leq 0.05$.

woody features are located towards the bottom of the plot. This relationship remained significant for farmland micro moths (Table S.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.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.8.).

4. Discussion

We 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

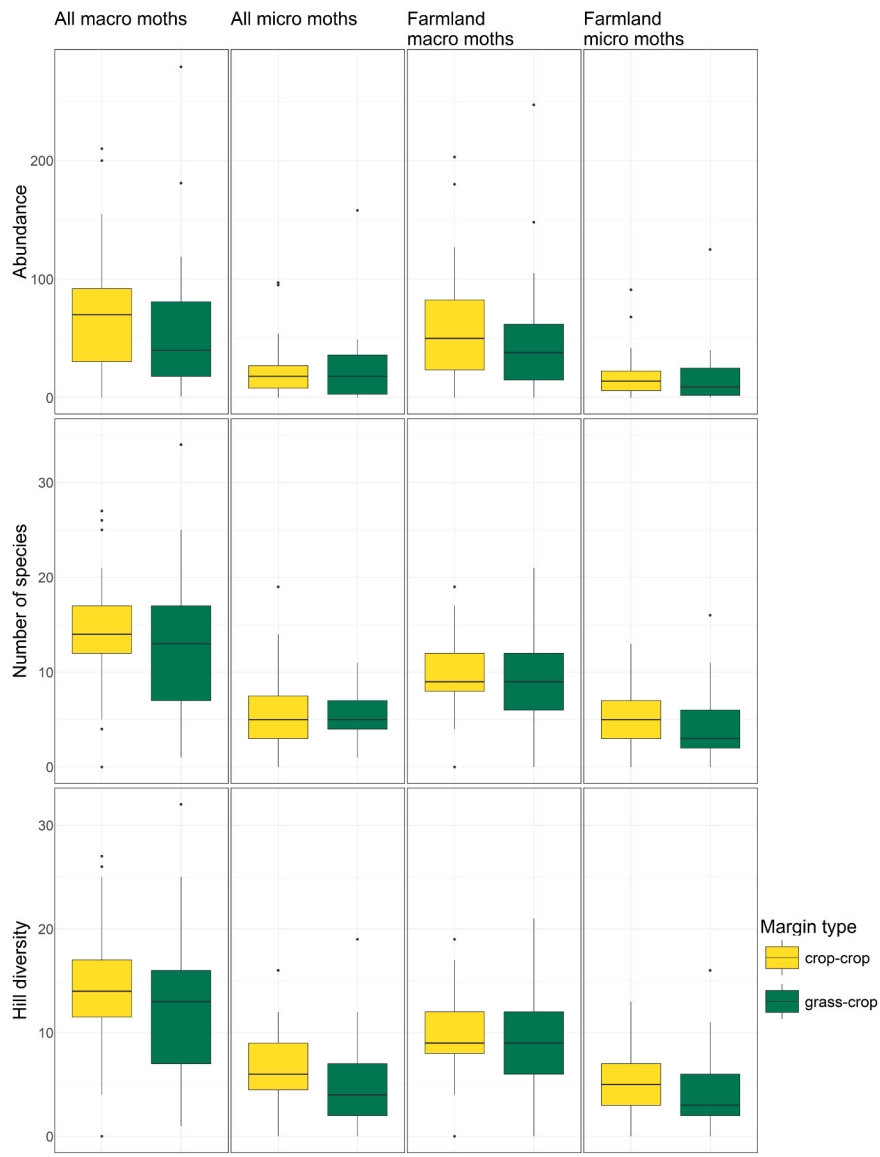

Fig. 6. Boxplots showing differences in moth abundance, species richness and diversity between crop-crop and grass-crop margins on mixed farms. Significance codes: (***) $p \leq 0.001$, (**) $p \leq 0.01$, (*) $p \leq 0.05$, ns > 0.1.

shaping both macro and micro moth communities.

4.1. Farming strategies

We 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, we found no suggestion that mixed farms included in our study were using less synthetic fertiliser compared with arable farms (Table S.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 our 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, we 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 our 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

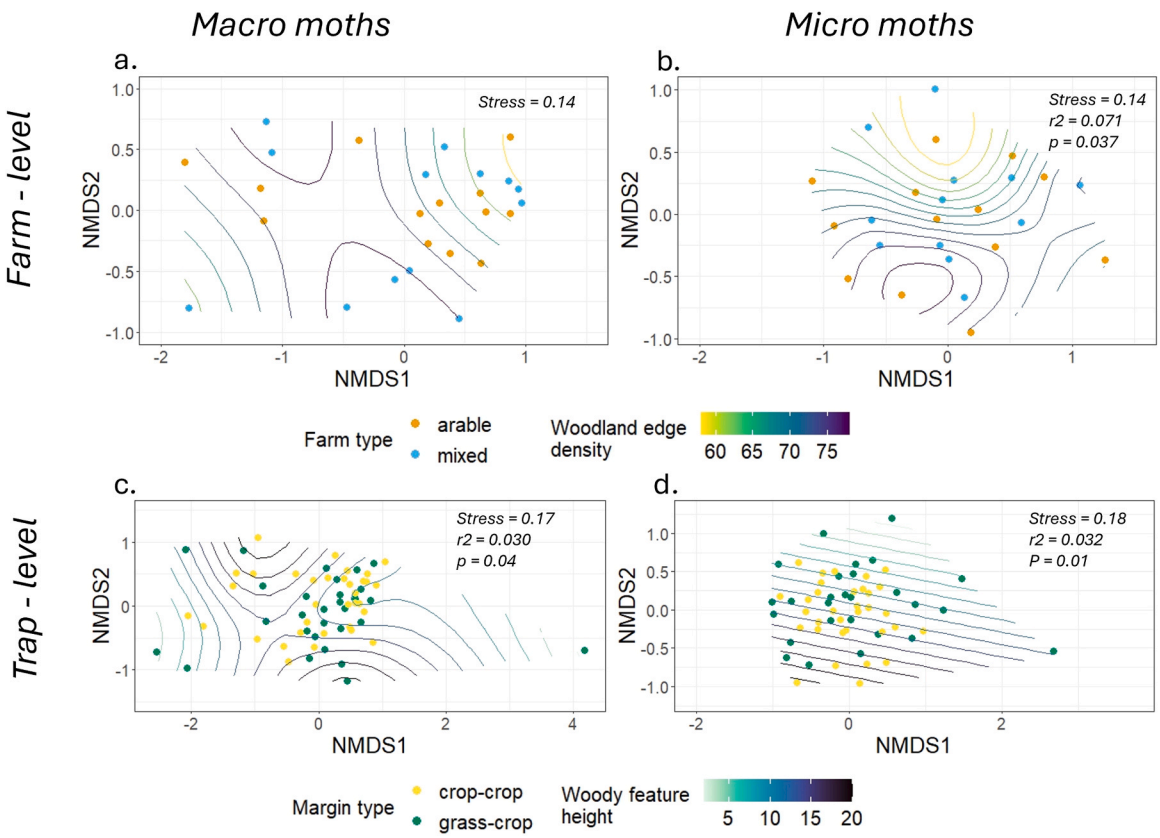

Fig. 7. NMDS plots of moth community composition at the farm scale and at the local scale for macro moths and for micro moths. Each point represents a moth community, with points that are closer together in the plot showing moth communities that are more similar in composition than those that are further 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.

diversity may not be influencing moths on our study sites, where semi-natural areas were low with a mean value of 1.5 % for the 1000 m 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 our own.

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 22 m 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 our knowledge our 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 our 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 our results highlight the importance of studying both macro and micro moths.

We also acknowledge that our 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, our 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.

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 our 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 our 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.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. We suggest that a range of structurally different woody features could help to increase macro and micro moth beta diversity in agricultural landscapes.

5. 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.

CRediT authorship contribution statement

Nick Littlewood: Writing – review & editing, Validation, Supervision, Software, Project administration, Methodology, Funding acquisition, Data curation, Conceptualization. **Kirsty J Park:** Writing – review & editing, Validation, Supervision, Resources, Project administration. **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.

Declaration of Competing Interest

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

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2025.109996.

Data availability

Data are available online at the University of Stirling's DataSTORE: http://hdl.handle.net/11667/244.

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