

Landscape woody features, local management and vegetation composition shape moth communities in extensively managed grasslands

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Abstract

1. Agricultural intensification has led to a dramatic impoverishment of biodiversity. Moths are not an exception: rapid declines of common and widespread species have been reported and it is still not clear which conservation measures should be applied to restore their populations.
2. We investigated how much of the variation in moth assemblages inhabiting extensively managed meadows in a region of high-intensity agriculture is explained by surrounding woody landscape features, meadow management and vegetation composition, and which specific variables are the most influential.
3. Results show that the percentage of forest and the length of hedgerows within a 250 m radius were especially important for forest macromoths, explaining 42% of variation in abundance and 23% of species richness, whereas meadow management played a relatively marginal role. The abundance of grassland macromoths was also positively influenced by the length of hedgerows in the landscape (combined with elevation it explained 10% of the variance), while it responded negatively to uncut refuge and to delayed mowing (7%). Regarding grassland macromoth species richness, the annual harvesting frequency was the main predictor (4%). In contrast, micromoth abundance was more influenced by meadow management, notably the date of the first cut (4%) and vegetation composition (8%, though not conclusive due to a single outlier), whereas landscape features explained nothing.
4. Altogether, these results demonstrate the importance of both woody features within farmed landscapes and biodiversity-friendly meadow management for the maintenance of integral moth communities.

KEYWORDS

agri-environment scheme, farmland biodiversity, hedges, landscape, lepidopteran, meadow, micromoth

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INTRODUCTION

The progressive intensification of agricultural practises during the second half of the 20th century has led to the spatially and temporally simplified landscapes that now dominate western European lowlands (Henle et al., 2008; Stoate et al., 2009). In these areas, semi-natural grasslands have become rare and isolated, often harbouring impoverished plant, bird and invertebrate communities (Poschod & Wallis DeVries, 2002; Wesche et al., 2012). Concerns about the impacts of agricultural intensification on farmland bird populations emerged decades ago (Carson, 1962); nonetheless, populations continue to decline (Heldbjerg et al., 2018; Knaus et al., 2019). The negative impact of modern management practises on invertebrates has also been widely reported; for example, on diurnal butterflies (Hannappel & Fischer, 2020; van Dyck et al., 2009; Warren et al., 2021; Wenzel et al., 2006) but also on a related but far less investigated group, moths (Fox, 2013; Mangels et al., 2017). Rapid declines, in a magnitude similar to butterflies and birds, of still common and widespread moth species are now observed throughout Europe (Conrad et al., 2006; Groenendijk & Ellis, 2011). Among endangered moth species, those that live in open-canopy forests and grasslands appear to be most affected (Pavlikova & Konvicka, 2012). It has been argued that even slight alterations of habitat quality or availability can have dramatic negative effects on moth demography (Jonason et al., 2013; Kadlec et al., 2009; Taylor & Morecroft, 2009).

As a corollary, targeted local conservation measures can benefit moths. For example it has been shown that field margins broader than 6 m – a widespread agri-environment scheme (AES) option in England – locally increase species richness of macromoths (Merckx et al., 2012), and their abundance if located in proximity to semi-natural chalk grasslands (Alison et al., 2016). Similarly, species richness of both macro- and micromoths, as well as the abundance of the latter, were significantly higher on Scottish farms under AES management compared to conventionally managed farms (Fuentes-Montemayor et al., 2011; see also Taylor & Morecroft, 2009). Furthermore, Fuentes-Montemayor et al. (2011) found that the percentage cover of surrounding semi-natural elements, such as rough grasslands and scrubs, was an important landscape predictor for both macro- and micromoth abundance and macromoth species richness, while Merckx et al. (2012) could establish similar positive effects in the presence of hedgerow trees. In a remote Mediterranean ecoregion of NW Portugal, de Miranda et al. (2019) found a higher forest macromoth diversity in abandoned farmland than in managed meadows, emphasising again the importance of scrub habitat for this group. In summary, moth abundance and species richness are higher in extensively managed grasslands compared to conventionally managed grasslands but are still strongly influenced by the surrounding environment. Yet, the relative contributions of all these factors, as well as that of local herbaceous plant composition are still unclear. This calls for specific research that can provide more concrete recommendations for conserving and restoring farmland moth communities.

The main aim of this study was to quantify and compare the effects of the surrounding woody landscape features, meadow

management and vegetation composition of extensively managed meadows on macromoth abundance and species richness, as well as on micromoth abundance. We took the opportunity of an ongoing field-scale, experimental study on the effects of four different mowing regimes upon meadow biodiversity (see Bruppacher et al., 2016; Buri et al., 2013; Buri et al., 2014; van Klink et al., 2017) to test moth responses to both landscape structural conditions and grassland management modes.

We hypothesised that a large proportion of the variation (R^2) observed in macromoth abundance and species richness would be explained by surrounding woody landscape features such as the amount of hedgerows and forest (Coulthard et al., 2016; Merckx et al., 2010; Merckx et al., 2012). In addition to a straightforward positive effect upon the guild of forest moths (de Miranda et al., 2019; Facey et al., 2014), we predicted that grassland macromoths would, to some extent, also benefit from woody features because these elements enhance the overall agricultural landscape heterogeneity, providing food sources and shelter for a majority of species (Benton et al., 2003; Diacon-Bolli et al., 2012; Steiner et al., 2014). For micromoths, which tend to be relatively less mobile than macromoths (Nieminen et al., 1999), we predicted comparatively stronger responses to meadow management and vegetation composition, rather than to woody landscape features (Merckx, Feber, Dulieu, et al., 2009). More specifically, we predicted a positive effect on micromoth and macromoth populations of late mowing as well as a reduced number of harvests per year as this provides more time to moths for accomplishing their life cycle (van Klink et al., 2019; Walter et al., 2007). In line with it, the presence of uncut refuges was further expected to benefit moths in general, as it provides continuity of shelter and food resources during the whole season, which diminishes caterpillar mortality (Cizek et al., 2012; Humbert et al., 2010; Kühne et al., 2015; Summerville & Crist, 2004; Šumpich & Konvicka, 2012).

Given that all meadows included in this study had been extensively managed for at least 10 years, and therefore all harboured a relatively diverse vegetation (on average 29 plant species per 16 m² area; see van Klink et al., 2017), the fraction of the variation (R^2) explained by plant species richness was expected to be low for all moth groups (Pöyry et al., 2009; Steiner et al., 2014). Finally, the percentage cover of forbs and legumes was expected to have positive effects on moths as they play the role of nectar providers, whereas the percentage cover of grasses was assumed to be neutral especially because grasses covered about 70% of the study grasslands.

MATERIALS AND METHODS

Study sites

The study was conducted in 48 extensively managed meadows spread in 12 regions across the whole western and central Swiss Plateau, consisting of four meadows each (in 2012, however, a meadow was lost when transformed into a gravel pit, so $n = 47$ for this study). The Swiss Plateau is a densely populated hilly lowland belt located

between the Alps and Jura mountain ranges, it is characterised by intensive mixed farming systems combining arable and livestock production with, nevertheless, 20%–30% of the area covered with semi-natural elements like forest patches and hedgerows. See Zingg et al. (2018) for more details on land cover of the Swiss Plateau as well as the illustration Figure S2.1b. There was a minimal distance of 5 km between two study regions and a minimal distance of 440 m between two meadows within a region, but all meadows of a region were located within 3.5 km of each other. Finally, meadows average size was 0.8 ha (range 0.3–1.7 ha). The geographical coordinates of the meadows are provided in Appendix S1, while a map with an overview of all study sites can be found in Appendix S2.

Meadow management

All investigated meadows were registered under Swiss agri-environment schemes (AES) and extensively managed since 2004 or before, with no fertilisation, no cut before 15 June (but without restriction on the number and frequency of subsequent cuts) and grazing permitted only in autumn. A quarter of our study meadows (i.e. 12 meadows) followed the above exact minimum AES requirements, whereas three different experimental mowing treatments were randomly allocated to each of the other three quarters and implemented continuously from 2010 onward: (1) first possible cut delayed to 15 July; (2) maximum of two cuts per year and at least 8 weeks between two successive cuts; (3) leaving a refuge uncut on 10%–20% of the area each time the meadow was mown. Yet, as our study looked at landscape structure in addition to meadow management mode, the present analysis relies on a simplified comparative – instead of fully experimental – approach, in which management characteristics were reduced to the following three factors: actual date of first mowing; number of harvests per year (which corresponded to the number of grass cuts a year plus one if autumn grazing took place); and presence of an uncut refuge. For the first two management variables, values averaged over the 4 years were used (Table 1).

Moth sampling

In 2014, moths were sampled three times, twice before any meadow was mown (the first sampling session was conducted between 25 April and 8 May and the second sampling session between 19 May and 26 May) and once after all meadows except meadows with delayed mowing had been mown (this third session was carried out between 26 June and 13 July), using light traps (Merckx & Slade, 2014; New, 2004). To reduce the action radius of the light traps, the top half of the surface of the 15 W black light bulbs was masked, resulting in approximately 7.5 W bulb power (see pictures C and D in Appendix S2). The light traps were installed 1.6 m above ground in the meadow centre. All meadows from the same study region were sampled during the same night, starting at dusk and lasting 5 h. Nights had to be dry with temperature above 8°C and maximum wind speed

TABLE 1 The different variables (or fixed effect) for landscape features, meadow management and vegetation composition included in the linear regression analyses.

Variables	Unit	Explanation
<i>Landscape features</i>		
Forest cover	(%)	250 m radius from meadow centre
Forest edges	(m)	250 m radius from meadow centre
Hedgerows	(m)	250 m radius from meadow centre
Elevation	(m)	Elevation a.s.l.
Meadow area	(m ²)	Total area of the meadow
<i>Meadow management</i>		
Age	Year	No of years since extensively managed
First cut	Julian day	Average from 2010 to 2013
Number of harvests		No of cut(s) plus autumn grazing (if presence) per year, average from 2010 to 2013
Uncut refuge	Yes/No	Presence of an uncut grass refuge
<i>Vegetation composition</i>		
Plant species richness		Number of herbaceous plant species
Non-legume forbs	(%)	Cover
Grasses	(%)	Cover
Legumes	(%)	Cover

of four Beaufort as in the study by Fuentes-Montemayor et al. (2011). Moths were euthanised with ethyl acetate and deep-frozen until identification. Macromoths were counted, identified to species level based on the study by Steiner et al. (2014) and grouped into three guilds: grassland, forest or ubiquitous species. Macromoths also included large-sized micromoth families like Limacodidae, as they are commonly included in macromoth studies (Potocký et al., 2018). Guilds were based on host plant preferences derived from the study by Mangels et al. (2017), who already used such a classification, and Steiner et al. (2014) for species not mentioned in the study by Mangels et al. (2017). Ubiquitous species included generalist moth species for which host plants occur in both grassland and forest habitats. Micromoths were only counted due to common-place identification challenges with this taxon. Finally, data of the three sampling sessions were pooled to obtain one sample per meadow.

Landscape variables

Landscape variables (see Table 1) were extracted from the Vector 25 database of the Swiss Federal Office of Topography, using QGIS and Spatialite software (Furieri, 2008; Quantum GIS Development Team, 2018) as described by Buri et al. (2014). Percentage of forest, forest edge and hedgerow lengths were quantified within a 250 m

radius of meadow centre. This radius has been chosen based on the findings by Fuentes-Montemayor et al. (2011) and to limit potential spatial autocorrelation due to overlapping radii within study sites.

Vegetation variables

In spring 2014, before mowing, vegetation relevés were conducted in each meadow on two 2 × 4 m plots (the duplication was intended to capture small-scale heterogeneity in vegetation composition; see figure 1 in the study by van Klink et al., 2017 for a graphical description). All vascular plant species were identified and their respective coverage estimated.

Plant species were classified in three functional groups: grasses (Poaceae, Juncaceae, and Cyperaceae), legumes (Fabaceae) and non-legume forbs (all other families). Data from the two plots were pooled for the species richness analysis and averaged regarding the percentage cover of grasses, legumes and non-legume forbs. Because of overlapping plant layers, the summation of the percent covers may exceed 100%.

Statistical analysis

The effects on moth communities of landscape features, meadow management and vegetation composition were analysed using linear mixed

TABLE 2 Summary of the LMM outputs for: (a) macromoth abundance; (b) macromoth species richness; (c) grassland macromoth abundance; (d) grassland macromoth species richness; (e) forest macromoth abundance; (f) forest macromoth species richness; and (g) micromoth abundance.

Model and fixed effect	Estimate	SE	df	p (> t)	Variance partitioning (adj. R ²)			
					(1) Land. feat.	(2) Mead. manag.	(3) Veget. comp.	(4) Study region
(a) Macromoth abundance (mean = 59.8; SD = 42.5)								
Intercept	63.37	11.11	11.62	<0.001				
Forest cover	10.37	5.03	38.73	0.046	0.100			
Hedgerows	13.91	4.16	35.14	0.002				
Refuge (yes)	-16.10	7.89	32.72	0.049		0.028		
Rand. effect	36.09							0.694
(b) Macromoth species richness (mean = 20.3; SD = 8.2)								
Intercept	20.26	1.39	10.38	<0.001				
Forest cover	3.89	1.15	39.73	0.002	0.250			
Hedgerows	3.30	1.05	40.30	0.003				
First cut	-1.95	1.07	37.97	0.076		0.074		
Number of harvests	-3.45	1.20	41.71	0.007				
Rand. effect	3.69							0.179
(c) Grassland macromoth abundance (mean = 37.2; SD = 29.7)								
Intercept	41.50	8.32	11.09	<0.001				
Hedgerows	8.58	2.57	33.60	0.002	0.098			
Elevation	-12.12	5.58	34.88	0.037				
First cut	-5.81	2.36	32.22	0.020		0.070		
Refuge (yes)	-16.72	5.44	34.16	0.004				
Rand. effect	27.45							0.800
(d) Grassland macromoth species richness (mean = 10.13; SD = 3.9)								
Intercept	10.13	0.82	10.73	<0.001				
Hedgerows	0.93	0.48	39.32	0.058	0.050			
First cut	-0.98	0.49	36.14	0.051		0.037		
Number of harvests	-1.38	0.57	41.76	0.021				
Rand. effect	2.49							0.387
(e) Forest macromoth abundance (log-scale) (mean = 9.3; SD = 8.8)								
Intercept	2.02	0.12	10.24	<0.001				
Forest cover	0.64	0.09	42.42	<0.001	0.420			
Hedgerows	0.29	0.08	40.27	0.001				
Number of harvests	-0.21	0.08	42.28	0.017		0.062		
Rand. effect	0.34							0.158

(Continues)

TABLE 2 (Continued)

Model and fixed effect	Estimate	SE	df	<i>p</i> (> t)	Variance partitioning (adj. <i>R</i> ²)			
					(1) Land. feat.	(2) Mead. manag.	(3) Veget. comp.	(4) Study region
(f) Forest macromoth species richness (log-scale) (mean = 5.8, SD = 4.0)								
Intercept	1.80	0.09	15.19	<0.001				
Forest cover	0.40	0.08	30.51	<0.001	0.331			
Hedgerows	0.27	0.07	42.91	0.001				
Refuge (yes)	-0.25	0.16	33.61	0.117		0.009		
Rand. effect	0.13							0.042
(g) Micromoth abundance (log-scale) (mean = 28.9; SD = 45.3)								
Intercept	2.79	0.26	10.54	<0.001				
Elevation	-0.31	0.20	27.79	0.121	0.011			
First cut	0.21	0.09	33.40	0.024		0.037		
Legume cover	-0.31	0.10	36.78	0.004			0.076	
Rand. effect	0.83							0.571

Note: For each model (a–g), the variables (fixed effects) retained after model selection based on AICc values are given. Prior to the analyses, all variables except *Refuge* were standardised (mean = 0 and SD = 1) to allow for direct comparison of the estimates. Definitions of each variable are provided in Table 1. Random effect (Rand. effect) reports the estimated standard deviation for the random intercept effect (i.e. study region). Significant *p* values are highlighted in bold. The second part of the table reports the results of the variance partitioning analysis. Adjusted *R*² values represent the fraction of variance explained uniquely by: (1) landscape features variables; (2) meadow management variables; (3) vegetation composition variables; and (4) the study region (the random effect in the LMMs). Finally, the mean number and standard deviation of moths trapped per meadow (three sampling sessions pooled) are also provided.

models (LMMs). Response variables were (a) macromoth abundance; (b) macromoth species richness; (c) grassland macromoth abundance; (d) grassland macromoth species richness; (e) forest macromoth abundance; (f) forest macromoth species richness; and (g) micromoth abundance. The initial full models included all landscape features, meadow management and vegetation composition variables as fixed effects (see Table 1), while random effects were the 12 study regions (accounting for potential spatial autocorrelation within region). Note that because percentage of forest and length of forest edges were highly correlated (*R* = 0.79), the latter was disregarded. The models were fitted using Gaussian error distribution and the response variables were log-transformed where necessary to achieve a normal distribution of the residuals (as indicated in Table 2). For each of the seven response variables, the model with best support was determined using the *dredge* function of the *MuMIn* package in R (Bartoń, 2015; Johnson & Omland, 2004). Hereby, all possible models (i.e. combinations of explanatory variables) are fitted and ranked according to the corrected Akaike's information criterion (AICc). To improve model convergence, continuous explanatory variables were standardised (mean = 0 and SD = 1). Model comparisons were based on maximum likelihood, but as recommended by Zuur et al. (2009), parameter estimates from models fitted with restricted maximum likelihood are reported for final inference. To estimate how much of the variance was explained by the explanatory variables retained in the best models, we performed a variance partitioning analysis using the *varpart* function of the *vegan* package (Oksanen et al., 2015). In brief, the *varpart* function partitions the variation of the response variable with respect to two to four explanatory tables using redundancy analysis ordination (RDA, see Borcard et al., 1992). Retained explanatory variables were filled in these tables according to their

attributes: (1) landscape features; (2) meadow management; and (3) vegetation composition (as in Table 1). Study region (the random effect in the LMMs) was added as an extra explanatory table.

As the results showed that the sampling regions were more influential than landscape features and local variables in explaining the observed variation (except for forest macromoth abundance), we suspected a large turnover of species (β -diversity) from a region to another. To investigate this hypothesis, the dissimilarity matrix of both taxonomic groups (grassland and forest macromoths) was calculated for each pairwise region using a binary (presence/absence) version of the Jaccard index. We opted for the Jaccard index as it represents a direct and easy to interpret proportional measure of species turnover (Anderson et al., 2011), which was computed with the *vegdist* function from the *vegan* package. Finally, a linear model was used to test whether both taxonomic groups statistically differ in their mean turnover (β -diversity). All analyses were performed using R 4.1.0 (R Core Team, 2020).

RESULTS

A total of 2810 macromoths and 1358 micromoths were trapped. Macromoths belonged to 147 species from the families *Drepanidae*, *Erebidae*, *Lasiocampidae*, *Limacodidae*, *Noctuidae*, *Nolidae*, *Notodontidae* and *Sphingidae* (Appendix S3). The six most common species of macromoths, representing 52% of the sample for their whole taxon, were *Noctuidae* typical of grassland: *Agrotis exclamationis* (449 individuals collected), *Charanyca trigrammica* (256), *Hoplodrina blanda* (112), *Mythimna pallens* (126), *Ochropleura plecta* (212) and *Xestia c-nigrum* (318, which was classified as ubiquitous species). On average (\pm SD),

30 (± 35) moths were sampled per meadow and night: 10 (± 19) micromoths and 20 (± 23) macromoths. Regarding macromoths, the average number of species sampled per meadow and night was 8 (± 6). *Smerinthus ocellata*, of which two individuals were caught in two different meadows, were the only national priority species encountered (no red list existing for moths in Switzerland). On average, the meadows were mown twice with a first cut on 29 June (range 15 June to 8 August). Regarding vegetation surveys, in total 155 plant species were recorded with an average of 29 (± 8) species per meadow. On average, 66% of the vegetation cover of a meadow consisted of grasses, followed by non-legume forbs (39%) and legumes (13%).

Macromoths

Table 2 provides a summary of the best-supporting models about the impact of landscape features, meadow management and vegetation composition variables on macro- and micromoth communities. Total macromoth abundance and species richness were best explained by the proportion of forest cover and the length of hedgerows within 250 m radius from meadow centre, as well as the presence of uncut refuge for abundance and the mean number of harvests per year for species richness (see Figures S4.1 and S4.2). The variance (adjusted R^2) explained by the landscape features and meadow management variables were,

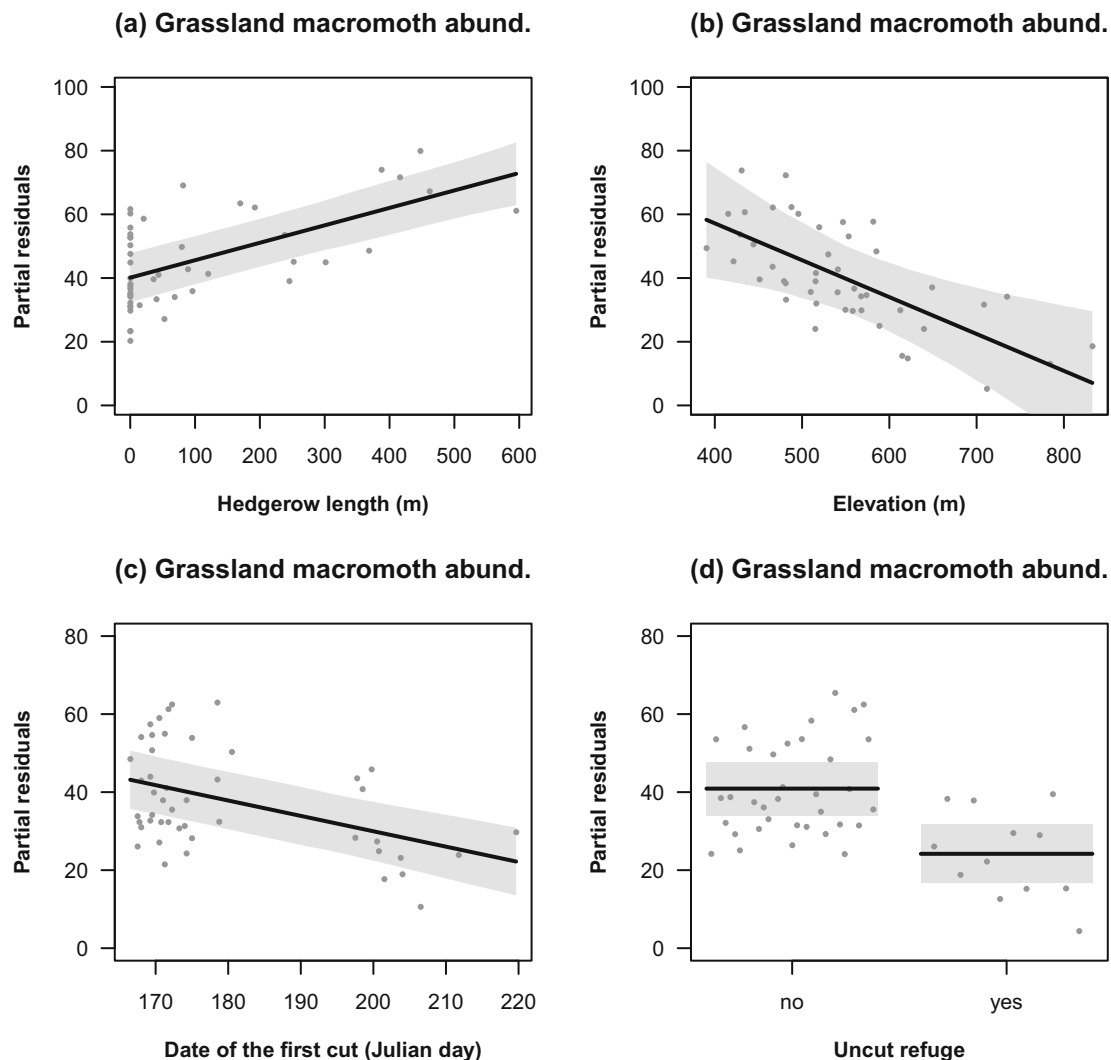


FIGURE 1 Relationships between grassland macromoth abundance and: (a) hedgerow length; (b) elevation; (c) the date the meadow was first cut (as day of the year, range from 166 = 15 June to 220 = 8 August); and (d) presence of an uncut refuge after mowing. Hedgerow length represents the total length of hedgerows found within a 250 m radius of meadow centre. Shown are the partial residuals (i.e. the residuals left after subtracting the influence of the other variables in the model) and predictions with 95% confidence intervals from the related LMMs presented in Table 2, though, for visual convenience, variables were set on the real scale. The intercept corresponds to the predicted conditional response when all other variables present in the model are set to their median values (for continuous variables) or most common category (i.e. no uncut refuge for the variable *Refuge*). Figures were generated using the *visreg* function from the *visreg* R package (Breheny & Burchett, 2017)

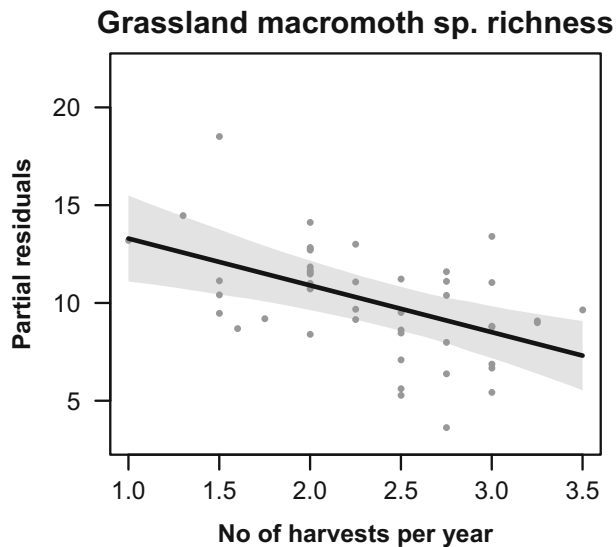


FIGURE 2 Relationships between grassland macromoth species richness and the number of harvests (mowing plus grazing events) per year. Plot characteristics as in Figure .1

respectively, 0.100 and 0.028 for macromoth abundance and 0.250 and 0.074 for macromoth species richness (Table 2). The adjusted R^2 of the study regions (i.e. the random effect in the LMMs) were 0.694 for abundance and 0.179 for species richness. These adjusted R^2 values represent the fraction of variance attributable to each explanatory table uniquely (i.e. landscape features variables, meadow management variables or study region in these cases). For grassland macromoth abundance, four variables were retained in the best model: hedgerow length, elevation, the date of the first cut and the presence of an uncut refuge (Figure 1, Table 2). Most of the variance was explained by the study region (0.800) followed by the landscape features (0.098) and the meadow management variables (0.070). Concerning grassland macromoth species richness, only the mean number of harvests per year was retained in the best model (Figure 2, Table 2). Similarly, most of the variance was explained by the study region (0.387) followed by the landscape features (0.050) and the meadow management variables (0.037). Forest macromoth abundance and species richness were best explained by the proportion of forest cover and the length of hedgerows within 250 m radius from meadow centre (Figures 3a,b and 4a,b, Table 2), as well as the mean number of harvests per year (for abundance; Figure 3c, Table 2). Contrary to grassland macromoths, most of the variances in forest macromoth abundance (0.420) and forest macromoth species richness (0.331) were attributable to landscape features. While meadow management explained 0.062 part of the variance in forest macromoth abundance and 0.037 part of the variance in forest macromoth species richness, and the study region 0.158 and 0.042, respectively (see Table 2).

Finally, the analysis of β -diversity using the binary (presence/absence) version the Jaccard index revealed that grassland and forest macromoths significantly differed in their species turnover from a region to another. Mean β -diversity (\pm SD) were 0.51 ± 0.11 for grassland macromoths and 0.76 ± 0.07 for forest macromoths (linear model: estimate = 0.25 SE = 0.01, $p < 0.001$). Note that here the

Jaccard index can be interpreted as the relative (proportional) species turnover from one region to another, that is, a value of 0.51 means that 51% of the species are different between both regions. A regression against distance between pairwise regions showed that β -diversity increased with distance for forest macromoths but not for grassland macromoths (Appendix S5).

Micromoths

Micromoth abundance was best explained by the date of the first cut and legume cover of the meadow vegetation composition (Figure 5). However, the negative effect of legume cover was driven by a single meadow in Orbe with 70% legume cover. Whereas there is no biological reason to remove this outlier, we confirm that the legume effect disappeared from the best model after removing this outlier from the data set, while the effect of the date of the first cut remained (results not shown). Variance partitioning analysis showed that the date of the first cut and legume cover explained, respectively, 3.7% and 7.6% of the variance in micromoth abundance, which was mostly explained by the study region (57.1%, see Table 2).

DISCUSSION

This study suggests that it is mostly landscape features such as percentage of forest and length of hedgerows within a 250 m radius, and, to a lesser extent, meadow management practises that best describe macromoth community in extensively managed grasslands. Depending on macromoth functional guild, landscape factors explained 5% (grassland macromoth species richness) to 42% (forest macromoth abundance) of the overall variance (based on variation partitioning with redundancy analysis ordination), whereas 1%–7% were explained by meadow management. In contrast, the less mobile micromoths have their abundance dictated primarily by local management and vegetation parameters, which in this study explained about 10% of their variance.

Landscape features

The crucial role played here by the surrounding woody landscape features on macromoth populations corroborates findings of agro-ecological research, carried out either on moths (Alison et al., 2017; Fuentes-Montemayor et al., 2011; Fuentes-Montemayor et al., 2012; Kivinen et al., 2006) or on butterflies (e.g. Flick et al., 2012; Merckx, Feber, Riordan, et al., 2009; Perović et al., 2015; Saarinen et al., 2005). Percentage of forest cover increased forest macromoth abundance and species richness, whereas the length of hedgerows around trapping sites positively influenced abundance and species richness of forest macromoths as well as grassland macromoth abundance. Together, these landscape features explained 42% of forest macromoth abundance and 33% of forest macromoth species richness. Hedgerows alone explained 5% of

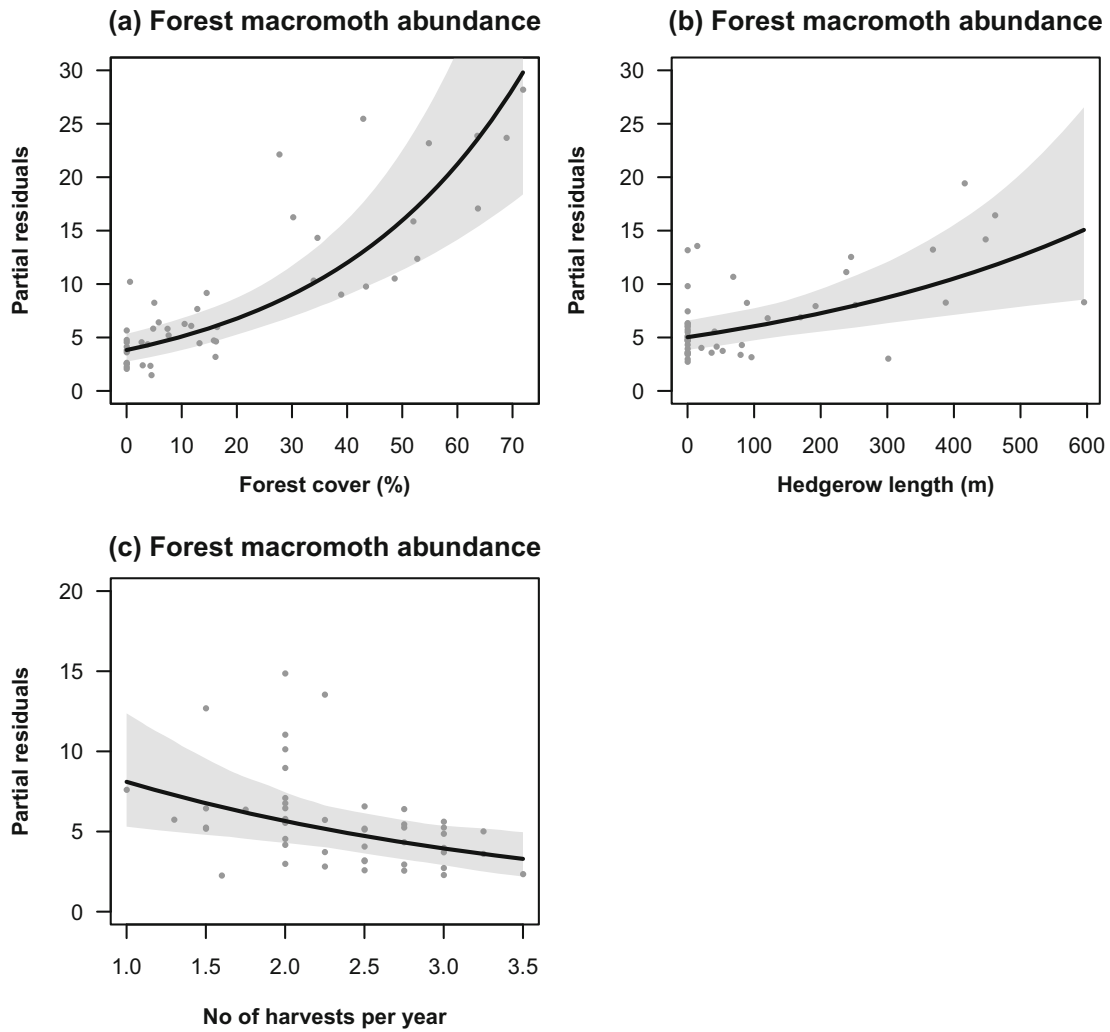


FIGURE 3 Relationships between forest macromoth abundance and: (a) percentage of forest cover; (b) hedgerow length; and (c) the number of harvests (mowing plus grazing events) per year. Forest cover represents the proportion of forest found within a 250 m radius of meadow centre. Other plot characteristics as in Figure 1

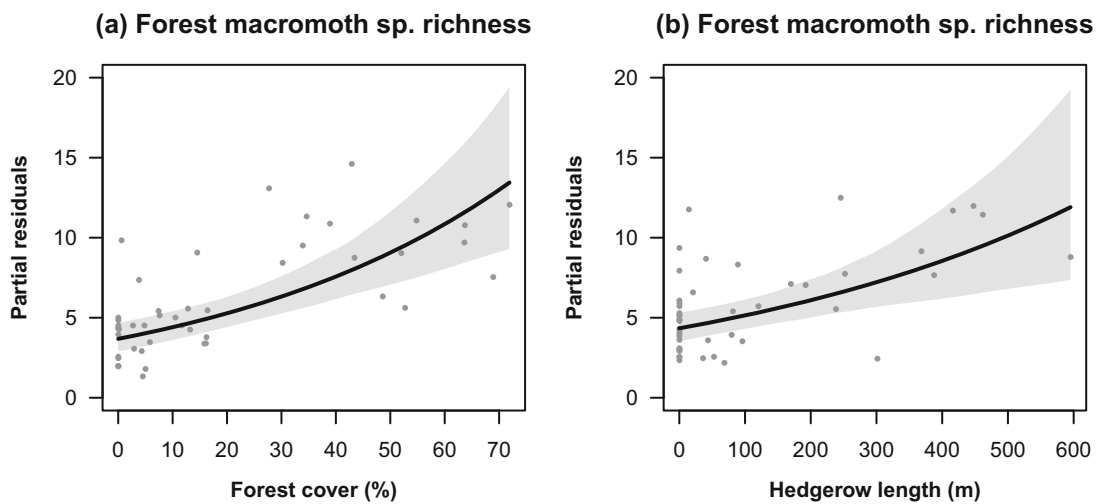


FIGURE 4 Relationships between forest macromoth species richness and: (a) percentage of forest cover; and (b) hedgerow length. Plot characteristics as in Figure 1

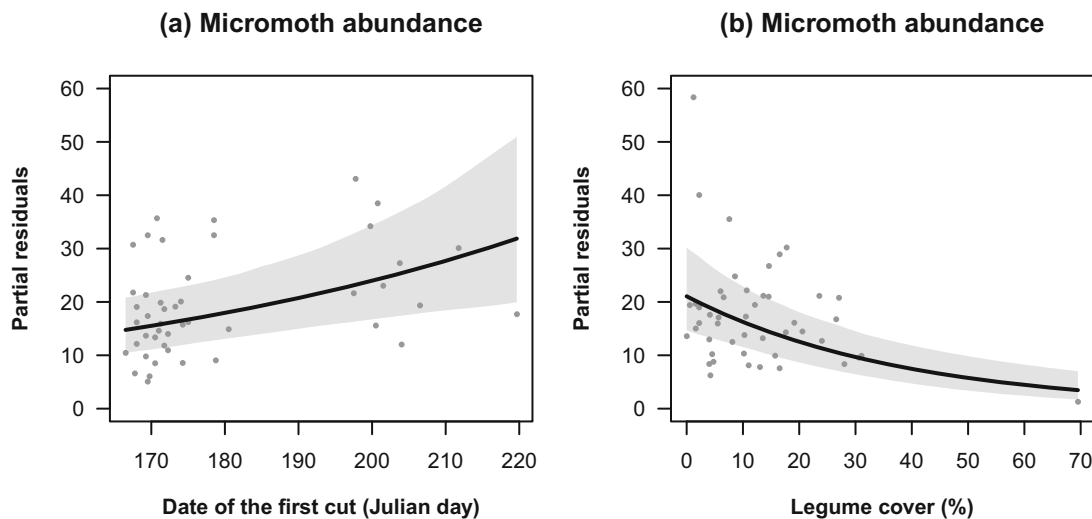


FIGURE 5 Relationships between micromoth abundance and: (a) the date the meadow was first cut (as day of the year, range from 166 = 15 June to 220 = 8 August); and (b) legume cover of the meadow vegetation composition. Plot characteristics as in Figure 1

grassland macromoth species richness, though not statistically significantly ($p = 0.058$) and, combined with elevation (negative effect), 10% of grassland macromoth abundance. This indicates that woody structures are important not only for forest macromoths but also for their open land counterparts. These effects were expected as a certain cover of forest fragments among farmland is known to boost butterflies and day-active moths (Bergman et al., 2018; Ekroos et al., 2010). Similarly, it has already been shown that hedgerows provide shelter and wind-protected corridors for both commuting and foraging moths, irrespective of their host plants (Coulthard et al., 2016; Merckx et al., 2010; Merckx, Feber, Riordan, et al., 2009). In addition, the majority of the encountered grassland macromoths were generalists whose caterpillars can readily feed on all sorts of herbaceous plants that are, in turn, often found in herbaceous field margins adjacent to hedgerows (Merckx et al., 2012; Steiner et al., 2014). Altogether, this emphasises that the conservation of Macrolepidoptera depends to a large extent on the wider habitat matrix heterogeneity (Ekroos et al., 2010; Prevedello & Vieira, 2010; Tschantke et al., 2005; Uhl et al., 2021). Our results show, however, that these same woody landscape features play no noticeable role for micromoth abundance within meadowland.

Our 12 study regions (see Study sites subsection) were separated by minimum 5 km and expanded over 200 km. While this had the advantage to encompass a large environmental gradient and make the results more generalizable, moth community tended to differ among regions, which may have weakened some relationships. Indeed, the β -diversity analysis revealed that species turnover between two regions was on average 51% for grassland macromoths and 76% for forest macromoths, confirming findings of Merckx et al. (2012) that forest macromoths are characterised by a higher β -diversity. Intriguingly, forest macromoths turnover increased with distance between two sites, while it did not for grassland macromoths. This difference might be due to the lower mobility of the former compared to the latter moth guilds (as in the study by Merckx et al., 2010), which would

also explain the general stronger response of forest macromoths to the direct surrounding landscape variables, especially in terms of percentage of variance explained (see also de Miranda et al., 2019).

Meadow management

Postponing the first mowing date from mid-June to mid-July was expected to be positive because it is likely to allow more invertebrates to achieve their reproductive and life cycles (Valtonen et al., 2006; van Klink et al., 2019; Walter et al., 2007). However, we could confirm this hypothesis only for micromoths, which benefitted from the delayed, mid-summer grass cut (4% of explained variation), but not for forest and grassland macromoth species, with the abundance of the latter even responding negatively to delayed mowing. The fact that grassland management plays a role for micromoths is not surprising. Šumpich and Konvička (2012), for instance, have demonstrated that management alone (mowing vs. abandonment) can explain up to 30% of the variation in micromoth communities inhabiting protected humid grasslands. Regarding macromoths, many of the species encountered in our study have late phenologies (e.g. *H. blanda*), if they are not simply bivoltine (e.g. *M. pallens*). Many may hence fly in June and occur as caterpillars or pupae in July when late mowing is performed. So they probably prefer a relatively earlier cut (mid-June), and no or a late second cut, or even grazing (see also Merckx, Feber, Dulieu, et al., 2009). In line with this hypothesis, the number of harvests per year (number of cuts plus grazing if occurring) had a negative effect on the species richness of grassland macromoths and abundance of forest macromoths: such a pattern has already been observed in several other taxonomic groups (Dover et al., 2010; Helden & Leather, 2004; Humbert et al., 2009). Former investigations also established that some moth caterpillars are particularly affected by grazing (Kruess & Tschantke, 2002; Littlewood, 2008; Pöry et al., 2005).

Concerning the expected benefit of leaving unmown grass refuges after each cut, results do not seem to support this hypothesis. They even show that the abundance of grassland macromoths and the species richness of forest macromoths were negatively affected by the presence of refuges. While we are not aware of any other study on the effects of leaving uncut grass refuges on moths, the negative response evidenced here contrasts with the positive effects obtained for butterflies (Bruppacher et al., 2016; Konvicka et al., 2008; Kühne et al., 2015), orthopterans (Buri et al., 2013; Humbert, Ghazoul, et al., 2012), and many other groups (see Buri et al., 2014; Cizek et al., 2012; Humbert et al., 2018). Note that we cannot exclude methodological shortcomings regarding samples taken after mowing, when the attractiveness of the light trap might be reduced in the meadows harbouring uncut refuges compared to meadows without refuges (moths may then stay in the refuge instead of moving around).

Vegetation composition

Among all vegetation descriptors considered in this analysis, only the percentage cover of legumes played a significant role, and actually a negative one for the abundance of micromoths. This does not necessarily mean that legumes are harmful to micromoths but could indicate that most micromoths rely on other host plants or sources of nectar. In addition, the negative trend was driven by one study site with both a high legume cover and a low micromoth abundance. Whereas there is no biological reason to ignore this outlier, the effect disappeared after removing it from the data set. Nevertheless, this again emphasises a stronger dependence of micromoth upon local site conditions compared to macromoths (Šumpich & Konvička, 2012; Uhl et al., 2022).

As regards macromoths, the majority of the species encountered were generalist foragers, which might explain the absence of effects of plant species richness (Alison et al., 2017). Alternatively or additionally, since all our study meadows had been extensively managed for at least the previous 10 years, they all harboured a relatively high plant diversity and cover of forbs, and thus nectar, much more so than in conventionally managed, high-intensity meadows (Knop et al., 2006; van Klink et al., 2017). Such favourable conditions might have provided insufficient contrast between our meadows to acknowledge the actual importance of vegetation composition (Uhl et al., 2020). Species like for instance *M. pallens*, occur mostly in non-fertilised grasslands (Steiner et al., 2014), which was definitely the case in all our 47 study meadows. Yet, the presence/absence of some specific host plants surely drives the presence/absence of some moth species (Axmacher et al., 2009; Saarinen et al., 2005).

Conclusion and conservation recommendations

This study suggests that the preservation of integral moth communities within cultivated landscapes necessitates hedges and forest patches in complementation to grasslands that are extensively

managed, such as those typically encountered within agri-environmental schemes (see also de Miranda et al., 2019). More specifically, macromoths would benefit most from such a heterogeneous mosaic while micromoths would profit from delayed mowing regimes. However, the latter measure appears to be potentially detrimental to macromoths in general, which emphasises that there is no single appropriate mowing window that suits all grassland organisms (Birkhofer et al., 2015; Cizek et al., 2012; Humbert, Pellet, et al., 2012). To avoid any such potentially counterproductive management schemes, the ultimate solution would be to maintain or create farmland matrices offering at the same time a sufficient landscape structural heterogeneity and a good variety, in space and time, of low-input meadowland mowing regimes. Finally, we remind that the focus of the study was mainly on spring and summer moth communities as field sampling stopped in July.

AUTHOR CONTRIBUTIONS

Isabel Kühne: Conceptualization (equal); data curation (lead); formal analysis (equal); investigation (equal); methodology (lead); writing – original draft (lead); writing – review and editing (equal). **Raphaël Arlettaz:** Conceptualization (equal); funding acquisition (lead); resources (lead); supervision (supporting); writing – review and editing (equal). **Jean-Yves Humbert:** Conceptualization (lead); data curation (supporting); formal analysis (equal); funding acquisition (supporting); investigation (equal); methodology (supporting); project administration (lead); resources (supporting); supervision (lead); validation (lead); visualization (lead); writing – original draft (supporting); writing – review and editing (lead).

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CONFLICT OF INTEREST

There are no conflicts of interest to be declared among the authors of the manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the “CESTES” database at <https://icestes.github.io/>, study id 50.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Support- ing Information section at the end of this article.

Appendix S1. Study sites and moths raw data.

Appendix S2. Study landscape and light trap pictures.

Appendix S3. List of the macromoth species.

Appendix S4. Total macromoth abundance and species richness in relation to different variables.

Appendix S5. Relationship between macromoth β -diversity and dis- tance between pairwise regions.

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