



Factors influencing moth assemblages in woodland fragments on farmland: Implications for woodland management and creation schemes

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ARTICLE INFO

Article history:

Received 10 January 2012

Received in revised form 27 March 2012

Accepted 17 April 2012

Keywords:

Agri-environment schemes

Habitat fragmentation

Habitat loss

Landscape

Lepidoptera

Micromoths

Macromoths

Woodland

ABSTRACT

As a consequence of long-term deforestation, woodland cover has been drastically reduced in the United Kingdom. The remaining woodland consists mainly of small, highly fragmented woodland patches within farmland. A number of agri-environment schemes aim to increase the amount and quality of woodland on agricultural land, but there is limited information on associations between moths and woodland characteristics which can be used to produce practical recommendations for woodland creation and management. We studied micro- and macromoth communities in woodland patches within farmland to assess the effects of woodland vegetation character and patch configuration. In addition, we measured the influence of the surrounding landscape to assess the potential importance of a landscape-scale management approach for moth conservation. In general, high tree species diversity and a high proportion of native tree species were related to higher moth abundance and species richness; there was a negative impact of grazing. Moth abundance and richness were higher in large woodland patches located close to other woodlands. Woodlands of compact shapes (with proportionally less edge exposed to the surrounding matrix) had higher numbers of 'woodland species', which were associated with woodland core habitat. Small woodland patches can potentially maintain relatively high moth abundance and richness, depending on their shape and proximity to other woodlands. Woodland extent was the most important landscape parameter influencing moths, mostly at relatively small spatial scales (≤ 500 m); macromoth 'woodland species' were influenced by woodland extent at larger spatial scales (≤ 1500 m) and are more likely to benefit from a landscape-scale management approach. Our results have important implications for the design and management of woodland patches of high conservation value within agricultural land.

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1. Introduction

As a consequence of long-term deforestation, woodland cover in Europe has been drastically reduced. In the United Kingdom (UK), the decrease has been so severe that at the beginning of the 20th century woodland was estimated to comprise *ca.* 5% of the land area (Mason, 2007). Programmes of afforestation over the last 50 years have increased this figure to approximately 12% cover (Mason, 2007). Much of this consists of forestry plantations, which in many cases have low species richness (exotic fast growing conifers) and low structural diversity (Mason, 2007). The remainder is highly fragmented and consists of a large number of relatively small woodland patches (<100 ha) within agricultural landscapes (Watts, 2006).

Moths occupy a variety of habitats, but many species (e.g. about two-thirds of British macromoths) occur regularly in woodlands and are associated with native tree species (Waring, 1989; Young,

1997). Ecological research and conservation efforts for Lepidoptera have been largely focused on butterflies. Relatively little attention has been given to macromoths and even less to the conservation status and habitat requirements of smaller micromoths, even though they comprise a large proportion of most local lepidopteran assemblages (Bland and Young, 1996). Many moth species have undergone severe population declines. In the UK, 62 species became extinct during the twentieth century (Fox et al., 2006) and many common and widespread macromoth species have shown significant population declines over the last few decades (Conrad et al., 2006). Moths have important roles as pollinators (Proctor et al., 1996), are an important food resource for many species of birds, bats and small mammals (Vaughan, 1997; Wilson et al., 1999) and a sensitive indicator group for agricultural intensification and forest quality (Jennings and Pocock, 2009; Kitching et al., 2000).

One of the most important threats to moths is habitat loss and fragmentation (Conrad et al., 2004), although changes in the structure, management and spatial configuration of woodlands have also been linked to declines of certain species (Broome et al., 2011; Fox et al., 2006). Moth abundance and species richness tend

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to increase with woodland patch size; woodland quality also influences moth populations, with herbaceous plant species richness, tree species diversity and tree basal area positively affecting moth abundance and species richness (Summerville and Crist, 2002, 2003, 2004; Usher and Keiller, 1998). Whilst the effects of patch configuration (e.g. shape and isolation) have rarely been assessed in these studies, Usher and Keiller (1998) found that compact patches had higher richness of woodland specialist species than elongated patches, while increased patch isolation reduced species richness of woodland macromoths. In addition, although positive effects of landscape heterogeneity, extent of open semi-natural environment and woodland up to 2 km from a locality have been reported for lepidopteran communities (Ekroos et al., 2010; Fuentes-Montemayor et al., 2011; Ricketts et al., 2001), the influence of the surrounding landscape has seldom been evaluated when studying moths in woodland fragments (but see Summerville and Crist (2004) who showed that increasing percentage cover of woodland within 1 km positively affects the abundance and species richness of woodland specialists). Many other taxa (e.g. small mammals and birds) are also affected by habitat fragmentation and exhibit patterns similar to those shown by moths (Fitzgibbon, 1997; Hinsley et al., 1995). In general, woodland patch size and availability at the landscape level are the most important factors influencing woodland specialists, whereas connectivity is most useful for generalist species for which patch size is not as important (Dolman et al., 2007; but see Bright, 1998).

In the UK, a number of agri-environment schemes (AES) which aim to increase the amount and quality of woodland on agricultural land have been in place for the past 20 years (Crabtree, 1996). However, recommendations for the creation and management of woodland to improve habitat for wildlife are strongly biased towards birds and mammals (e.g. Blakesley and Buckley, 2010), often disregarding smaller taxa (e.g. arthropods; but see Anonymous, 2007). In addition, the value of these woodland patches, in terms of biodiversity gains, is rarely assessed (but see Crabtree, 1996). Here, we examine both micro- and macromoth communities in woodland patches within agricultural landscapes to assess the effects of woodland vegetation character (e.g. tree species richness), patch configuration (e.g. size and shape) and surrounding landscape (e.g. proportion of woodland cover) on moth assemblages. In particular, we addressed three specific questions:

1. Do moth abundance and species richness relate to woodland vegetation character and patch configuration and, if so, to which specific attributes?
2. Does the surrounding landscape influence moth populations in woodland patches and, if so, at what spatial scale?
3. What is the relative importance of woodland vegetation character, patch configuration and surrounding landscape for enhancing moth populations (e.g. is local management of woodlands sufficient or is a landscape-scale management approach necessary for moth conservation)?

Given that micromoths are usually characterised by low mobility (Nieminen et al., 1999), they might be more influenced by the local habitat, and by patch isolation, compared to high mobility species (e.g. certain macromoths such as Noctuids), which may be more affected by habitat factors at larger scales (Merckx et al., 2009, 2010; Tscharrtkte et al., 2002). Therefore, we expect the relative importance of vegetation character, patch configuration and surrounding landscape to differ between micro- and macromoths. Furthermore, given that woodland specialists are more affected by woodland habitat quality and quantity than generalist species (Summerville and Crist, 2008), we expect this group to show stronger associations with the woodland character than other species.

2. Methods

2.1. Site selection and sampling design

Ordnance Survey digital maps (EDINA Digimap Ordnance Survey Service) were used to select 34 woodland patches within agricultural land in central Scotland (Fig. 1). All woodland patches were at least 60 years old (EDINA Historic Digimap Service) and ≥ 1 km from each other; they were selected based upon their size (from 0.1 up to 30 ha) and shape (ranging from compact to complex; Appendix A). Woodlands of different sizes were evenly surveyed throughout the duration of the field season and across the study area, avoiding any seasonal and spatial bias. Broadleaved woodlands and woodlands consisting of a mixture of conifer and broadleaved trees were selected given that they resemble semi-natural systems, whereas woodlands consisting purely of conifer plantations were excluded from the site selection process because they are often composed mainly of exotic tree species and are of comparatively low conservation value to biodiversity (Mason, 2007). All sites were surveyed for vegetation and nocturnal moths once during the summers of 2009 (June–August, 20 sites) and 2010 (May–July, 14 sites). We recognise that a single visit to each site provides only a coarse description of local moth assemblages. We adopted this approach in order to maximise the number – and to cover a wider range – of sites surveyed when attempting to determine the factors influencing moth assemblages in woodland fragments.

Vegetation surveys were conducted along transects of 100 m in length. Transects within a woodland patch were located in an area considered to be representative of the whole site (after exploration and visual assessment of the woodland); one transect was used for patches of 0.1–3 ha, two transects for patches of 3–10 ha, and three transects for patches of 10–30 ha. Points were established every 15 m along each transect and the following data were collected using the point-centred quarter method (Southwood and Hendersson, 2000): tree species richness, tree density and tree basal area (only trees ≥ 7 cm in diameter at breast height were measured). Each point also served as the corner of a 10 m \times 10 m quadrat – which was used to visually assess understory cover (%) using the Domin scale (Kent and Coker, 1992) – and a 2 m \times 2 m quadrat – used to visually determine the dominant ground cover type. Vegetation surveys were conducted no more than 2 weeks before the nocturnal moth surveys.

Moths were collected using portable 6 W heath light traps powered with 12 V batteries, which were activated 15 min after sunset and switched off after 4 h (the duration of the whole night period during the shortest summer night in the study area) using automatic timers. This allowed us to standardise the duration of the surveys throughout the season, and ensured that species flying at dusk and night were surveyed regardless of the duration of the night. Species flying at dawn were most likely missed, as traps were turned off before dawn (even during the shortest nights). Surveys were only conducted in dry weather, when temperature was ≥ 8 °C and wind force \leq Beaufort scale 4. Two traps were used in woodland patches of 0.1–3 ha, four traps in patches of 3–10 ha, and six traps in patches of 10–30 ha. The traps were ≥ 100 m apart from each other to prevent the lights from interfering with each other (Merckx et al., 2009). If the woodland patch was too small to allow for this distance between traps, we ensured trees or shrubs interrupted visibility between the lights (shortest distance between traps *ca.* 50 m). At each patch, an equal number of traps were located at the edge (≤ 2 m from the edge) and the interior (as far away from the edges as possible) of the woodland. When more than one ‘edge’ trap was used, we positioned these on different sides of the woodland patch to capture a wider variation of the

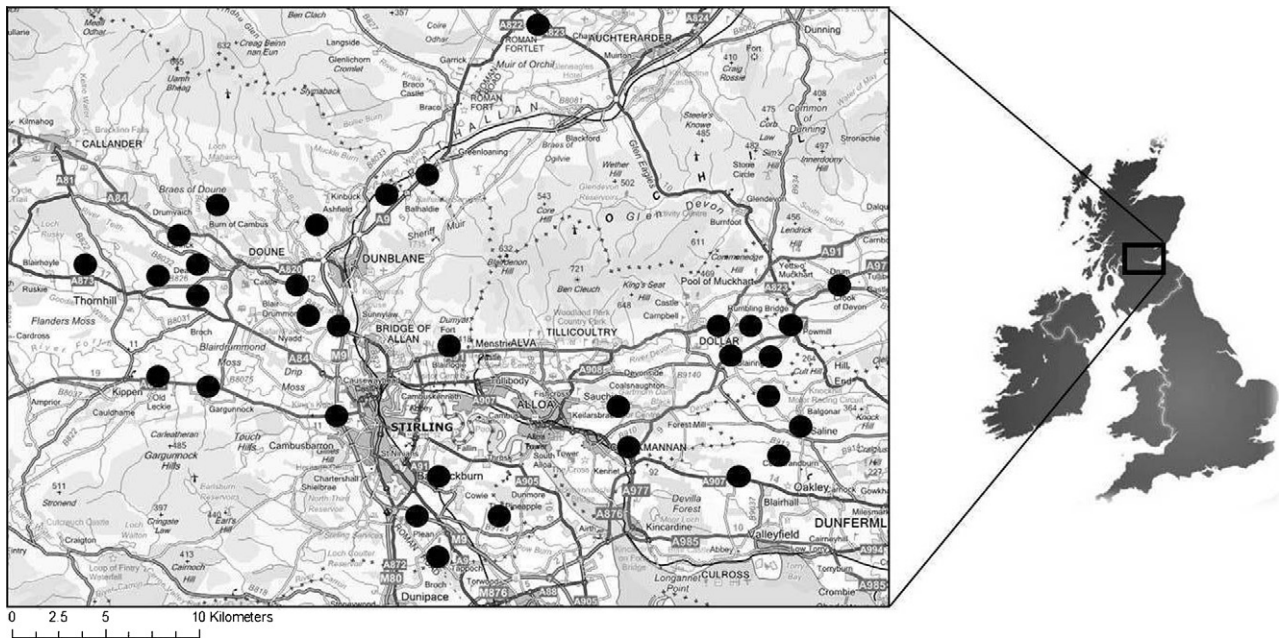


Fig. 1. Map of central Scotland showing approximate locations of woodland patches (black dots) surveyed during 2009/2010 (map produced using Carto, EDINA Digimap Ordnance Survey Service).

surroundings. The collected insects were euthanised and stored for later identification; individuals were dissected to examine genitalia whenever species identification required it. Moth species for which woodland is listed as the main habitat where species occurs and/or for which the larval food is a woody plant – according to Emmet and Heath (1991) and Waring and Townsend (2003) for micro- and macromoths, respectively – were considered to be strongly associated with woodland and assigned to the ‘woodland species’ guild.

2.2. Landscape analysis

We used ArcGIS 9.2 (ESRI, 2006) to create circles of 250 m, 500 m, 1000 m, 1500 m, 2000 m, 2500 m and 3000 m radius around the centre of each woodland patch. The smallest radius (250 m) covers the dispersal distances of low mobility moth species, the intermediate radii (e.g. 1.5 km), the dispersal distances of many common moth species, and the largest radius (3 km) approximates an upper limit to dispersal distances of more mobile non-migratory moth species (Merckx et al., 2009; Nieminen et al., 1999). Using data from OS MasterMap Topography Layer (EDINA Digimap Ordnance Survey Service) we reclassified the landscape within each circle into six biotope types: (i) urban areas (buildings, structures and roads); (ii) farmland; (iii) water (inland and tidal water); (iv) semi-natural environment (rough grassland and scrub); (v) scattered trees (refers to large areas covered by scattered trees, rather than to individual trees scattered across the landscape); and (vi) woodland (coniferous, deciduous and mixed trees). We then used Fragstats 3.3 (McGarigal et al., 2002) to calculate the proportion of land covered by each biotope type and a landscape heterogeneity index (Shannon diversity) within each circle.

2.3. Data analysis

We calculated diversity indices for micro- and macromoths using PAST (Hammer et al., 2001). We selected the α log series diversity index because of its good discriminant ability, its low

sensitivity to sample size and the fact that a number of previous studies have shown the index to be particularly suited to the description of moth populations (e.g. Magurran, 1988).

All statistical analyses were conducted using R version 2.11 (R Development Core Team, 2010). We performed Generalised Linear Mixed-Effects Models (GLMMs; Zuur et al., 2009) to determine which of the woodland character variables evaluated had an influence on moths. We used total values per trap (e.g. moth abundance, richness or diversity) as response variables ($n = 126$); therefore, the unit used for analyses remained the same even when sampling effort differed amongst sites of different sizes. Based on published literature on the ecology of woodland moths, we selected the following potential explanatory variables to be included in the starting models: (i) vegetation character variables: woodland type, tree species richness, relative abundance of native tree species, tree density, average tree basal area, understory percentage cover, dominant ground cover type, surrounding matrix type and presence or absence of in-site grazing; and (ii) patch configuration variables: woodland patch size (and its quadratic term to consider a potential non-linear effect), woodland patch shape, woodland patch isolation, trap location (woodland interior vs. woodland edge) and their respective two-way interactions. See notes in Appendix A for a full description of each variable. Date and temperature at sunset were included as covariates. A correlation matrix of all potential explanatory variables was created to check for possible collinearity between predictors; variables were considered to be strongly correlated if Pearson correlation coefficient ≥ 0.6 and $P \leq 0.05$. ‘Woodland type’ and ‘native trees’ were the only two strongly correlated variables, with broadleaved woodlands having a higher proportion of native trees than mixed woodlands; only one of these predictors (the one most strongly correlated with the response variable in turn) was included in the starting models. ‘Site’ and ‘year’ (‘site’ nested within ‘year’) were originally included in the models as random (grouping) factors, but because variation between years was negligible (variance approximated zero) this factor was excluded and only ‘site’ was used. All continuous variables were standardised following Schielzeth (2010) in order to allow meaningful comparisons of

the relative importance of predictors within a model, and interpretation of main effects where these are involved in interactions. Models were fitted using Poisson errors where the response variables were counts (e.g. moth abundance and species richness) and Gaussian errors (on log transformed data to achieve normality where necessary) for continuous variables (e.g. moth diversity). A backwards step-wise approach to model simplification was adopted, using $P = 0.05$ as a criteria for factor retention or removal. Models were also assessed using Akaike's information criterion (AIC; Akaike, 1974) at each simplification step. For all response variables the model selected by the stepwise approach matched the model with the lowest AIC value; we therefore present the results of the simplified models. All models were validated by visual examination of residuals (Crawley, 2007). These models are referred to as 'woodland character' models hereafter.

The effect of the surrounding landscape on moths was assessed in two steps: Firstly, we used linear regression analyses to evaluate the effect of each landscape parameter at different spatial scales on moth abundance, richness and diversity. We used mean values per trap for each woodland patch as response variables (log transformed to achieve normality where necessary; $n = 34$) and Gaussian error types. Secondly, we selected the landscape parameter that explained the highest overall variation in moth communities (highest R^2 value from linear regressions averaged across spatial scales) and added it, at each landscape scale, to the final 'woodland character' models (see above). We compared the models without any landscape metrics against the new models incorporating landscape metrics to assess whether they provided a better fit to the data, based on AIC values and significance tests which compare deviance values between models (χ^2 test; Zuur et al., 2009).

We calculated an index of dissimilarity using PAST (Hammer et al., 2001) to assess whether micro- and macromoth species composition differed between woodland interior and woodland edge and whether these differences were influenced by patch configuration metrics – patch size (and its quadratic term), patch shape, patch isolation, and their respective two-way interactions. We selected the Bray–Curtis dissimilarity index because it has been extensively used in ecological studies and can be easily interpreted (Waite, 2000). We used the total abundance of each species collected at each site (all 'interior' traps pooled together vs. all 'edge' traps) to obtain a dissimilarity value for each woodland site ($n = 34$). Linear models were fitted using Gaussian error types on log transformed data.

3. Results

We identified a total of 34 tree species (Appendix B). Tree species richness ranged from 2 to 15 per site; tree density ranged from 181 to 2512 trees per ha and average tree basal area from 0.03 to 0.43 m². Dominant ground cover types included 'grass', 'litter', 'bare ground', 'ferns', 'herb' and 'moss' (for analysis purposes, the latter four were grouped in the 'other' category because they were the dominant ground cover type in ≤ 2 sites). Appendix A summarises the characteristics of each site.

We collected a total of 1674 micromoths, belonging to 66 species (Table C1 in Appendix C) and 14 families, and 3518 macromoths, belonging to 146 species (Table C2 in Appendix C) and eight families. Of these, 62 macromoth and 25 micromoth species are strongly associated with woodland habitat (see Section 2) and were analysed as separate groups because they are likely to show stronger responses to woodland character. Eighteen moth species (all macromoths) in our samples are classed as common but rapidly declining and are of special conservation concern (Fox et al., 2006).

3.1. Effects of woodland vegetation character and woodland patch configuration

After accounting for the effects of date and temperature, moth abundance, richness and diversity were significantly influenced by variables related to both woodland vegetation character and woodland patch configuration (Table 1).

Micromoth abundance was positively related to the relative abundance of native trees and the percentage cover of understorey in a woodland patch. In-site grazing had negative effects on micromoth abundance and species richness (fewer individuals and fewer species in sites where grazing stock was present). Micromoth abundance and species richness increased with woodland patch size (Fig. 2a and b) and decreased with patch isolation (Fig. 3a and b), with more moths and more species collected in large patches, and in patches located close to other woodlands. Micromoth abundance was higher within the woodland interior than at the edge. 'Trap location' was involved in an interaction with 'woodland isolation', indicating that the negative effect of woodland isolation on micromoth abundance and species richness was stronger at the edge than in woodland interior. Micromoth species richness was higher in broadleaved than in mixed (broadleaved and conifer mix) woodland patches. Micromoth diversity was only influenced by the dominant ground cover type – 'grass' and 'litter' had lower diversity than 'other' (based on visual examination within this group, 'moss' < 'herbs' < 'ferns' < 'bare ground').

Micromoths assigned to the 'woodland species' guild (see Section 2) showed stronger associations with woodland character than all micromoth species (i.e. there was a higher number of significant predictors for their abundance and richness; Table 1). In-site grazing had strong negative effects on both abundance and richness of micromoth 'woodland species'. Tree species richness, the relative abundance of native trees and tree basal area were positively related to this group's abundance and richness. Micromoth 'woodland species' abundance was negatively related to the percentage cover of understorey and influenced by the dominant ground type; 'grass' and 'litter' had higher moth abundance than 'other' (within this group, 'bare ground' < 'moss' < 'herbs' < 'ferns'). Woodland configuration influenced micromoth 'woodland species' abundance and richness, which were higher in larger woodland patches (Fig. 2d and e) and in patches of compact shapes. Woodland isolation had negative effects on this group's abundance (Fig. 3d), which was also higher in the woodland interior than at the edge. A significant interaction between 'trap location' and woodland size indicated that the positive effect of patch size on the abundance of woodland micromoths was stronger in the woodland interior than at the edge (Fig. 2d). A significant interaction between 'trap location' and woodland shape indicated that, in compact patches, micromoth 'woodland species' were more abundant in woodland interior than at the edge, whereas this difference was non-existent in woodland patches of complex shapes.

Macromoth abundance and species richness were positively affected by tree species richness and by the relative abundance of native trees in a woodland patch. Of dominant ground types, 'grass' and 'litter' had higher abundances and species richness than 'other' (within this group, 'bare ground' < 'herbs' < 'moss' < 'ferns'). In-site grazing had negative effects on macromoth abundance, richness and diversity (fewer moths, fewer species and less diverse communities in sites where grazing stock was present). There were fewer species and a lower abundance of moths in sites surrounded by arable land than in sites surrounded by pastoral or mixed (pastoral and arable mix) land. Woodland size was positively related to macromoth abundance (Fig. 2f) – the same (marginally-significant) trend was observed for species richness and diversity (Fig. 2g and h) – whereas woodland isolation was negatively related to macromoth abundance and richness (Fig. 3f and g). Significant

Table 1

Summary table showing significance values, parameter estimates \pm SE (for main effects only, no interactions) and goodness of fit (model R^2) of the 'woodland character' models. Non-significant predictors are not shown. The effects of categorical variables with more than one level ('matrix type' and 'dominant ground') are discussed in the text. Surrounding woodland cover was incorporated to the 'woodland character' models at a later stage to assess the importance of a landscape-scale management approach; the most relevant spatial scale (the one that produced the model with the lowest AIC value) and its correspondent parameter estimates (\pm SE) and model R^2 values are indicated (see Table D1 in Appendix D for further details).

	Woodland vegetation character									Woodland patch configuration								Landscape					
	Date ^{a,b}	Temperature ^b	Woodland type ^{c,d}	Matrix type ^c	In-site grazing ^c	Tree species richness ^b	Native trees ^b	Tree basal area ^b	Understorey cover ^b	Dominant ground ^c	Woodland size ^b	Woodland shape ^b	Woodland isolation ^b	Trap location ^{c,e}	Trap location + Wood size	Trap location + Wood shape	Trap location + Wood isolation	Woodland size + Woodland shape	Woodland size + Woodland isolation	Model R^2 (%) ^f	Surrounding woodland cover ^g	Most relevant spatial scale (m)	Model R^2 (%) ^g
Micromoth abundance	1.27 \pm 0.25***	ns	ns	ns	-1.10 \pm 0.55*	ns	0.42 \pm 0.21*	ns	0.56 \pm 0.22*	ns	0.57 \pm 0.26*	ns	-0.41 \pm 0.23 [†]	0.53 \pm 0.06***	ns	ns	**	ns	ns	74.97	0.67 \pm 0.31*	500	75.17
Micromoth richness	0.70 \pm 0.14***	ns	-0.67 \pm 0.27 [†]	ns	-0.74 \pm 0.33*	ns	ns	ns	ns	ns	0.36 \pm 0.15*	ns	-0.26 \pm 0.15 [†]	ns	ns	ns	*	ns	ns	52.09	ns	-	-
Micromoth diversity	0.26 \pm 0.07***	0.14 \pm 0.07 [†]	ns	ns	ns	ns	ns	ns	***	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	32.03	0.15 \pm 0.07 [†]	250	34.65
Micromoth abundance (woodland species)	1.62 \pm 0.19***	ns	ns	ns	-4.07 \pm 0.58***	0.41 \pm 0.10***	0.50 \pm 0.15**	0.70 \pm 0.16***	-0.66 \pm 0.14***	*	0.64 \pm 0.24**	-1.07 \pm 0.20***	-0.36 \pm 0.14**	0.39 \pm 0.16*	*	**	ns	ns	ns	73.34	0.61 \pm 0.18***	500	74.55
Micromoth richness (woodland species)	1.33 \pm 0.24***	ns	ns	ns	-2.78 \pm 0.55***	0.20 \pm 0.11 [†]	0.49 \pm 0.19*	0.67 \pm 0.18***	ns	ns	0.99 \pm 0.14***	-0.37 \pm 0.20 [†]	ns	ns	ns	ns	ns	ns	ns	59.56	ns	-	-
Macromoth abundance (all species)	0.45 \pm 0.08***	ns	ns	*	-0.91 \pm 0.27***	0.26 \pm 0.11 [†]	0.49 \pm 0.12***	ns	ns	***	0.87 \pm 0.34*	ns	-1.60 \pm 0.46***	-0.13 \pm 0.04***	ns	ns	***	ns	**	59.85	ns	-	-
Macromoth richness (all species)	0.39 \pm 0.06***	ns	ns	**	-0.89 \pm 0.19***	0.23 \pm 0.07***	0.35 \pm 0.08***	ns	ns	**	0.39 \pm 0.22 [†]	ns	-0.71 \pm 0.30*	ns	ns	ns	ns	ns	*	55.66	0.28 \pm 0.10**	500	57.11
Macromoth diversity (all species)	1.90 \pm 0.70***	ns	-3.89 \pm 1.66 [†]	ns	-4.42 \pm 2.04*	ns	ns	ns	ns	ns	1.38 \pm 0.81 [†]	ns	ns	ns	ns	ns	ns	ns	ns	42.27	ns	-	-
Macromoth abundance (woodland species)	ns	ns	ns	*	-1.13 \pm 0.51*	0.54 \pm 0.21*	0.54 \pm 0.19**	-0.33 \pm 0.17*	ns	ns	ns	ns	-0.93 \pm 0.30**	0.31 \pm 0.06***	ns	ns	*	*	ns	64.81	1.17 \pm 0.45*	250	65.28
Macromoth richness (woodland species)	0.22 \pm 0.09*	ns	ns	**	-1.33 \pm 0.30***	0.45 \pm 0.11***	0.36 \pm 0.11***	ns	ns	*	ns	-0.28 \pm 0.11**	-0.58 \pm 0.15***	0.28 \pm 0.09**	ns	ns	*	ns	ns	57.29	0.26 \pm 0.10*	1500	58.97

^a Significance codes: **** $P \leq 0.001$, *** $P \leq 0.01$, ** $P \leq 0.05$, * $P \leq 0.1$ and 'ns' $P \geq 0.1$.

^b Standardised parameter estimates are shown for continuous variables.

^c Non-standardised parameter estimates are shown for categorical variables.

^d Negative values indicate a negative effect of 'mixed' woodlands (with respect to 'broadleaved').

^e Negative values indicate lower moth abundance/richness in woodland interior than at woodland edge.

^f R^2 values for models with a Gaussian error distribution were calculated with the formula: $1 - (\text{Residual Sum of Squares}/\text{Total Sum of Squares})$. Pseudo- R^2 values for models with a Poisson error distribution were calculated with the formula: $(\text{deviance explained by model}/\text{null deviance}) * 100$ (Zuur et al., 2009). Pseudo- R^2 values are not adjusted for the number of explanatory variables included in a model.

^g R^2 value after incorporating surrounding woodland cover at the most relevant spatial scale to the 'woodland character' models.

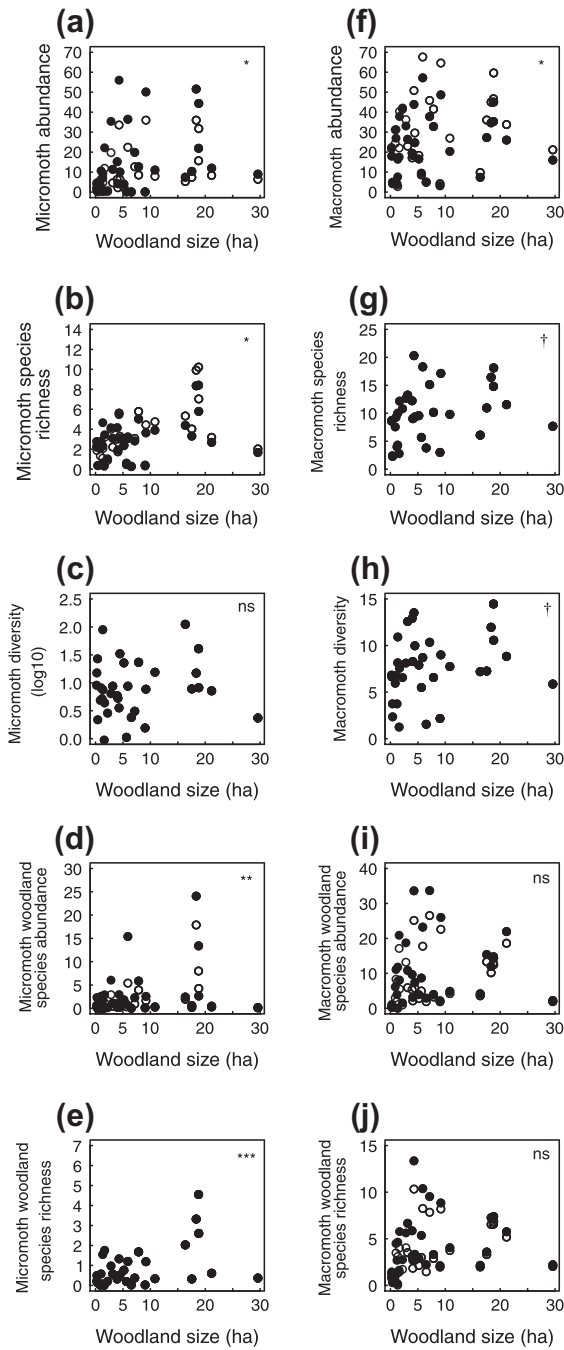


Fig. 2. Effect of woodland patch size and trap location (woodland interior vs. woodland edge, closed and open circles respectively) on micromoth (a, b and c) and macromoth (f, g and h) abundance, species richness and diversity. 'Woodland species' abundance and richness are shown separately (d and e for micromoths, i and j for macromoths). Fitted values produced by the final GLMMs for each response variable are shown. Only one type of circle is shown for models where trap location and its interaction with other predictors were not significant. Significance codes for woodland patch size are shown at the top right corner of each plot: **** $P < 0.001$, *** $P < 0.01$, ** $P < 0.05$, * $P < 0.1$ and 'ns' $P \geq 0.1$.

interactions between 'woodland size' and 'woodland isolation' indicated that whereas small woodlands generally have lower macromoth abundance and richness, these increase if the patch is located close to other woodlands. Macromoth abundance was higher at woodland edge than in woodland interior. A significant interaction between 'trap location' and 'woodland isolation' indicated that the negative effect of woodland isolation on macromoth abundance was stronger at the woodland edge than in the interior.

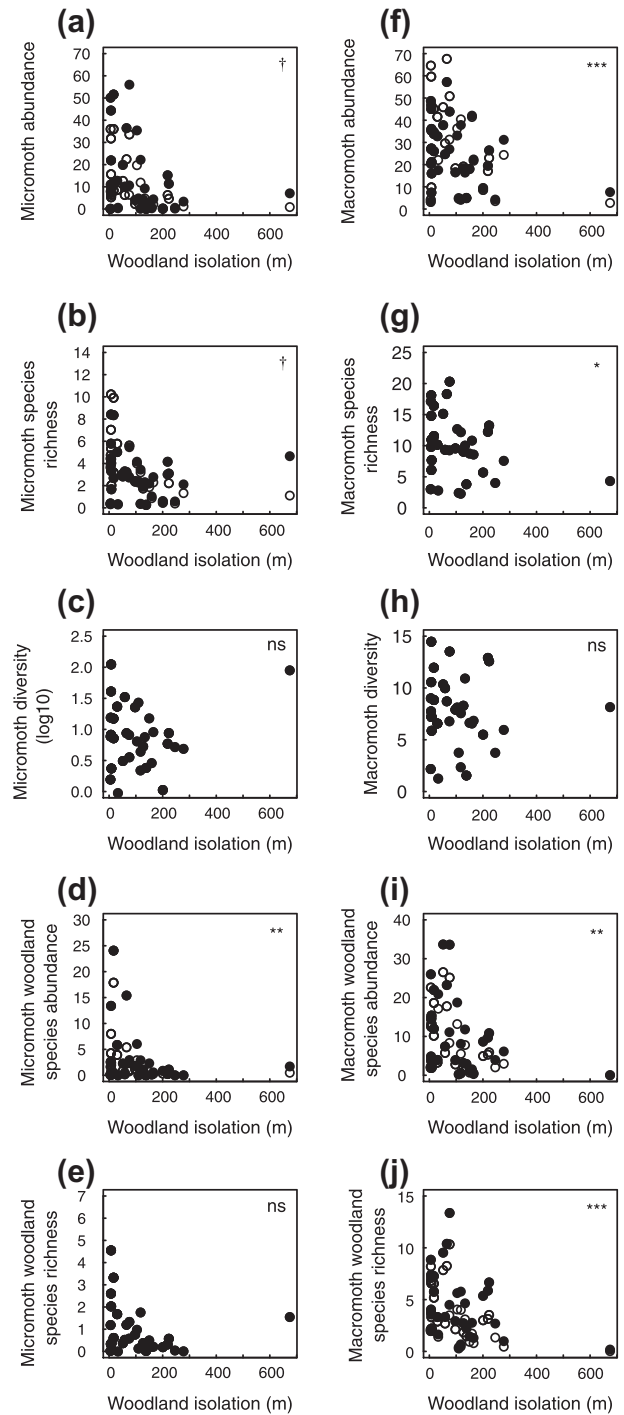


Fig. 3. Effect of woodland isolation (metres to closest patch) and trap location (woodland interior vs. woodland edge, closed and open circles respectively) on micromoth (a, b and c) and macromoth (f, g and h) abundance, species richness and diversity. 'Woodland species' abundance and richness are shown separately (d and e for micromoths, i and j for macromoths). Fitted values produced by the final GLMMs for each response variable are shown. Only one type of circle is shown for models where trap location and its interaction with woodland isolation were not significant. Significance codes for woodland isolation are shown at the top right corner of each plot: **** $P < 0.001$, *** $P < 0.01$, ** $P < 0.05$, * $P < 0.1$ and 'ns' $P \geq 0.1$.

Macromoth diversity was affected by woodland type (higher in broadleaved than in mixed woodland patches).

Macromoth 'woodland species' (those strongly associated with woodland) responded to vegetation character variables in a similar way to all macromoth species (Table 1). Tree species richness and

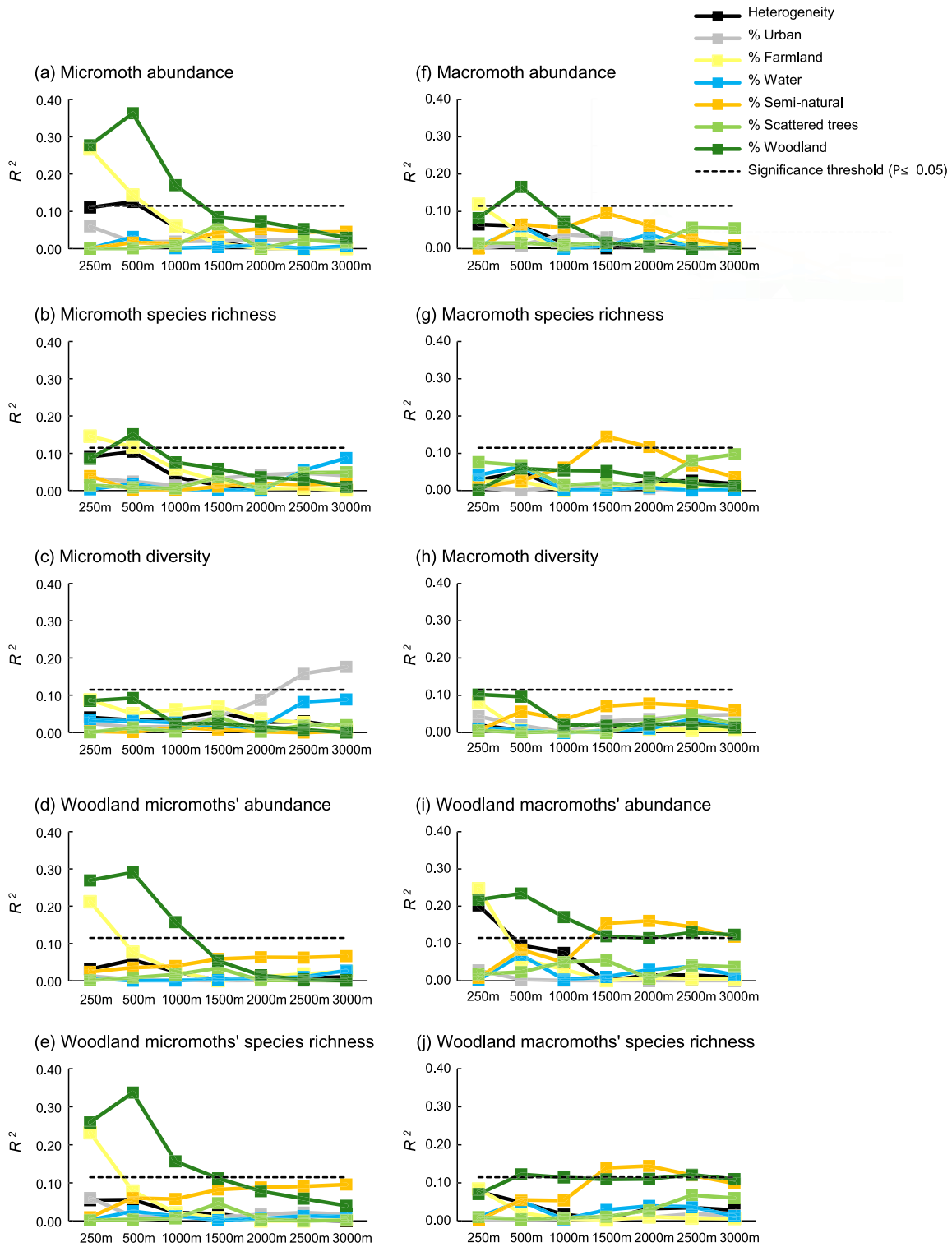


Fig. 4. R^2 values obtained from linear regression analyses between the percentage of land covered by each biotope type at several spatial scales and: (a) micromoth abundance, (b) micromoth species richness, (c) micromoth diversity, (d) micromoth ‘woodland species’ abundance, (e) micromoth ‘woodland species’ richness, (f) macromoth abundance, (g) macromoth species richness, (h) macromoth diversity, (i) macromoth ‘woodland species’ abundance and (j) macromoth ‘woodland species’ richness. We used mean values per trap as response variables ($n = 34$).

relative abundance of native trees had positive effects on macro-moth ‘woodland species’ abundance and richness. Tree basal area was negatively related to the number (but not abundance) of macro-moth ‘woodland species’. The dominant ground type affected the richness of ‘woodland species’ – ‘grass’ and ‘litter’ had more species than ‘other’ (within this group, ‘bare ground’ < ‘herb’ < ‘moss’ < ‘-

ferns’). In-site grazing had negative effects on the abundance and richness of ‘woodland species’, and there were fewer species and a lower abundance of moths in sites surrounded by arable land than in sites surrounded by pastoral or mixed land. The response of ‘woodland species’ to woodland configuration variables was somewhat different to that of all macro-moths (Table 1). A

significant interaction between woodland size and shape indicated that small woodland patches with complex shapes have the lowest abundance of 'woodland species'; however, abundance was relatively high in small woodlands with compact shapes and in large woodlands with complex shapes. Woodlands with complex shapes also had reduced 'woodland species' richness. Woodland isolation had negative effects on both abundance and richness of macro-moth 'woodland species' (Fig. 3i and j). However, significant interactions between 'woodland isolation' and 'trap location' indicated that the negative effects of isolation were stronger at woodland edge than in interior. The overall abundance and richness of 'woodland species' were higher in the woodland interior than at the woodland edge.

The species composition of both micro- and macromoths differed between woodland interior and woodland edge (Bray–Curtis dissimilarity index $\neq 0$; $t = 10.06$, $P < 0.001$ for micromoths; $t = 12.29$, $P < 0.001$ for macromoths). In the case of macromoths, these differences were caused by changes in the abundance and richness of 'woodland species' collected in interior vs. edge; in total 693 individuals belonging to 55 species strongly associated with woodland were collected in woodland interior (representing 43.2% in abundance and 45.5% in species richness of the total macromoth catch in interior traps), as opposed to 543 individuals from 46 species collected at woodland edge (representing 28.4% in abundance and 38.0% in species richness). Woodland patch configuration – woodland size ($t = 2.65$, $P = 0.015$), its quadratic term ($t = -2.35$, $P = 0.029$) and a marginally significant interaction between patch size and shape ($t = 2.06$, $P = 0.052$) – affected the similarity of micromoth (but not macromoth) species collected in woodland interior vs. edge. Woodland interior and woodland edge were more dissimilar (in terms of micromoth species composition) in larger woodland patches, although the interaction between woodland size and shape indicated that edge and interior are more similar in small woodlands with complex shapes and less similar in small patches with compact shapes.

3.2. Effects of the surrounding landscape

In general, linear regression analyses indicated that the percentage cover of woodland and semi-natural environment showed the strongest (positive) relations with moth abundance and species richness (Fig. 4). The percentage cover of farmland and the landscape heterogeneity index were also significantly related (negatively and positively, respectively) to moth abundance and richness, but only at relatively small scales (e.g. 250 and 500 m). The percentage cover of urban areas related only to micromoth diversity (positively) at large scales (e.g. 2500 and 3000 m). Given that the percentage cover of woodland was the landscape parameter that significantly related to more response variables (seven out of ten) and at more spatial scales (e.g. significantly related to 'woodland species' abundance at all spatial scales), we selected this as the landscape parameter to include in the 'woodland character' models. After incorporating this landscape metric to the 'woodland character' GLMMs, the percentage cover of woodland in the surrounding landscape significantly improved the models for most response variables at least at one spatial scale (Tables 1 and D1 in Appendix D). The models with the lowest AIC values were usually those which incorporated woodland cover at the 250 and 500 m scales. However, for 'woodland species' richness the model with the lowest AIC was the one which incorporated the proportion of woodland cover at a larger spatial scale (1500 m; Tables 1 and D1 in Appendix D). The results of similar analyses incorporating landscape metrics into the 'woodland character' GLMMs, but using other parameters (percentage cover of 'semi-natural environment' and 'urban areas') instead of 'woodland' are presented in Tables D2 and D3 in Appendix D.

4. Discussion

Lepidoptera are one of the most abundant and diverse insect orders; yet, macromoths at least, are relatively easy to sample and identify. Many moth species have been badly affected by habitat loss and fragmentation (Conrad et al., 2004; Fox et al., 2006; New, 2004), but relatively little is known about appropriate woodland management for this taxa. For these reasons, they are ideal for a study of this nature. We assessed the effects of woodland vegetation character, patch configuration and surrounding landscape on assemblages of both macromoths and the relatively poorly studied micromoths. Moths were significantly influenced by variables related to woodland vegetation character, woodland patch configuration and the surrounding landscape. Our results contribute to a better understanding of the effects of habitat loss and fragmentation on biodiversity and have important implications for the design and management of woodland patches of high conservation value within agricultural landscapes.

Variables related to the woodland vegetation character had an influence on both micro- and macromoth abundance and richness. In general, woodlands composed of broadleaved trees only (no conifers) and a large number of tree species supported high moth abundance and species richness. Tree species richness/diversity has been recognised in previous studies as one of the most important predictors for moth abundance and species richness (Summer-ville and Crist, 2004; Usher and Keiller, 1998). However, we also found the relative abundance of native tree species in a woodland patch to be of higher importance in most cases, presumably because non-native trees are unlikely to serve as food-plants for native moth species. Many native tree species (e.g. *Betula* sp., *Quercus* sp. and *Salix* sp.) have large numbers of moth species associated with them (i.e. feeding on them), although this is not always the case and there are native trees (e.g. *Fagus sylvatica*) which support relatively few moth species, comparable in number to those supported by non-native trees (e.g. *Acer pseudoplatanus*; Young, 1997). The dominant ground cover type was also an important predictor for some response variables; sites where grass or litter was the dominant ground cover type had higher moth abundance and species richness than sites dominated by 'other' ground cover. A high percentage of understory cover was beneficial (for micromoth abundance only), probably because it increases structural complexity and provides shelter. Conversely, micromoth 'woodland species' were more abundant in mature woodland patches (i.e. with large average tree basal areas) with little understory.

Characteristics related to woodland management also had an influence on moths; for instance, the presence of grazing stock in a site consistently had strong negative effects on moth communities. Grazing has been linked to changes in vegetation structure and composition (Stewart and Pullin, 2008) and its detrimental effects on moths have been noted in previous studies (e.g. Young and Barbour, 2004). However, the negative effects of grazing are not necessarily even across all moth species (Littlewood, 2008). In this study we found that sites surrounded only by arable land had lower macromoth abundance and fewer species than sites adjacent to pastoral or mixed fields, probably because an arable matrix is more homogeneous than a mixed or pastoral matrix.

Variables related to the spatial configuration of woodland patches had a profound impact on moth assemblages. Their relative importance was usually higher than that of vegetation character variables, particularly for macromoths. In general, both micro- and macromoth abundance and species richness were higher in large woodland patches located close to other woodlands. Arthropods are one of the taxa that best fulfil the theoretical expectations of greater species richness within larger fragments (Debinski and Holt, 2000). Previous studies show that the size of a woodland patch

appears to be one of the most important factors influencing species abundance and richness of different taxa (e.g. plants – Usher et al., 1992; birds – Hinsley et al., 1995), including moths (Summerville and Crist, 2003, 2004; Usher and Keiller, 1998), whereas the spatial configuration of the fragmented woodland seems to be less crucial (i.e. for birds – Dolman et al., 2007; Lee et al., 2002; McGarigal and McComb, 1995; plants – Usher et al., 1992). However our results show that woodland isolation in particular has strong negative effects on moths, probably because our study was conducted in a highly fragmented landscape (see also Usher and Keiller, 1998).

The responses of micro- and macromoths to the configuration of a woodland patch were somewhat different; although the two groups were affected by woodland size and isolation, for micromoths the former was more important than the latter, whereas for macromoths the opposite was observed. The negative effects of isolation were noticeable at smaller distances on micro- than on macromoths (i.e. micromoth abundance and richness decreased drastically above 100 m, whereas for macromoths the decrease was more gradual). For low mobility species (such as most micromoths) even short distances between woodland patches might act as dispersal barriers, increasing the relative importance of the size of their existing patch; this would probably result in micromoth populations being more dissimilar between woodland patches in the landscape (although we did not directly assess this). Significant interactions between 'woodland isolation' and 'trap location' (e.g. for micro- and macromoth abundance) indicated that the negative effects of isolation are stronger at the woodland edge than in woodland interior; presumably moths concentrate in woodland interior in highly isolated patches which do not offer dispersal opportunities, but make a more extensive use of woodland edges in sites which are close enough to other woodlands for them to disperse. The interactions between woodland patch size and isolation (significant only for macromoths) suggest that even small woodland patches can be beneficial for moths if they are located in proximity to other woodlands, which may act as sources of individuals/species to colonise nearby woodland patches. This observation – along with the overall importance of woodland isolation on moth communities – highlights the importance of incorporating aspects of spatial configuration in the creation of new woodlands during afforestation programmes.

The shape of the woodland patch was important particularly for woodland species (both micro- and macromoths), indicating that patches of compact shapes (with proportionally less edge exposed to the surrounding matrix) sustain a larger number (and larger populations, in the case of micromoths) of woodland species. Even though woodland shape *per se* did not affect the abundance of macromoth woodland species, it was involved in an interaction with woodland size; this highlights the importance of designing patches of compact shapes, especially when the patch to be created is small. Usher and Keiller (1998) also found that only moth species dependent upon woodland habitat show a relationship to shape, and suggested that this group of moths benefits from large woodland core habitat in woods of compact shapes. This is supported by our observations of higher richness and abundance of woodland species in woodland interior than at woodland edge, and suggests the existence of edge effects experienced by this group of moths. These apparent edge effects could potentially derive from a sampling effect (i.e. with traps located at the edge broadcasting *ca.* 50% of light into woodland and therefore sampling a smaller area than those located in woodland interior). However, the fact that patches of compact shapes (i.e. with proportionally less edge exposed to the surrounding matrix and more core habitat) generally had higher abundance and richness of 'woodland species' suggests the existence of 'true' edge effects, where the physical conditions at the edges affect the abundance and distribution of a species (Murgia, 1995). Edge effects have been identified as one of the main driving forces behind changes in insect populations in forest frag-

ments (Didham et al., 1996; Ewers et al., 2007; Ewers and Didham, 2008). Conversely, the abundance (but not richness) of all macromoth species was higher at woodland edge than in interior; this observation is most likely driven by a few abundant species, well adapted to agricultural environments (cf. species replacement hypothesis in Summerville and Crist, 2003, 2004).

Micromoth assemblages also differed between woodland interior and edge. These differences were accentuated by woodland size and shape. Micromoth species composition was more dissimilar between interior and edge in large woodland patches, indicating that traps located in the interior of small woodland patches are still influenced by edge effects. The interaction between size and shape indicated that edge and interior moth communities are more similar in small woodlands with complex shapes than in small patches with compact shapes, but the effect of shape was not noticeable in large woodlands. This shows that there are micromoth species associated with woodland core habitat which would benefit from large woodlands, and even from small woodlands of compact shapes. Summerville and Crist (2001, 2004) maintain that small (2–25 ha) woodland fragments can support many moth species if the habitat within them is good, whereas Usher and Keiller (1998) identify woodlands under 1 ha as not able to support characteristic communities of woodland moths, and woodlands of more than 5 ha as generally able to support more stable moth communities. Our results showed that woodlands <1 ha were indeed poor in species richness and abundance, while woodlands >5 ha had the highest values; however, relatively small patches (e.g. woodlands between 1 and 5 ha) seem to contain relatively large moth populations. This study and work by others (e.g. Ekroos et al., 2010) highlight the importance of increasing habitat availability and connectivity for habitat specialists (such as macromoth 'woodland species') and poor dispersers (such as many micromoths) to avoid biotic homogenisation in intensively cultivated landscapes with simplified landscape structure.

Both micro- and macromoth communities were influenced to some extent by the surrounding landscape. They were influenced by the percentage cover of woodland in the surrounding landscape at relatively small spatial scales (≤ 500 m), suggesting that local habitat management (or a landscape management at this spatial scale) would be suitable for moth conservation. Macromoth 'woodland species' richness, however, was influenced by woodland cover at larger spatial scales, the most relevant being 1500 m. These findings are in accordance with those of Ricketts et al. (2001) and Summerville and Crist (2004), who found that the amount of nearby woodland cover (within 1–1.4 km) positively affects moth abundance and richness. The total amount of woodland in the landscape has been recognised as being more important than woodland patch size or spatial pattern in other animal groups (i.e. birds; Dolman et al., 2007; Lee et al., 2002; McGarigal and McComb, 1995). Our observations suggest that macromoth 'woodland species' in particular would benefit from a wider landscape-scale management of woodland habitat. Conservation strategies are increasingly incorporating the concept of habitat networks in an attempt to minimise the effects of habitat fragmentation and conserve woodland biodiversity (Quine and Watts, 2009; Watts, 2006). Our results highlight the importance of management plans which perceive the landscape as a whole, and emphasise the need to take into account the surrounding landscape and the location of a woodland patch within it. In addition to producing practical recommendations to be incorporated in woodland management plans, our findings can be applied to woodland creation plans at the landscape scale (e.g. using spatial data to identify target areas for woodland creation) which would contribute to the design of better landscapes for woodland moths (ongoing work from the authors). Finally, many of the patterns we observed on moths are similar to those displayed by taxa such as small mammals and birds (e.g.

Fitzgibbon, 1997; Hinsley et al., 1995); therefore, recommendations drawn from our results are likely to create woodland patches valuable not only for moths, but also for other biodiversity.

4.1. Limitations

(i) *Temporal variations*: Each site was surveyed only once, which provides only a coarse description of local moth assemblages. However, we ensured that weather conditions were relatively similar during surveys and that these were randomised so that woodland patches of different character (e.g. size and isolation) were evenly surveyed throughout the season (Appendix A). In addition, previous studies have shown that patterns of moth community composition due, for example, to patch area effects, remain consistent despite seasonal species turnover (Summerville and Crist, 2003). Therefore, temporal variations are unlikely to have influenced the patterns detected during our study and the conclusions drawn from them. (ii) *Trapping effects*: Even though light trapping is the most effective technique for general moth recording (in terms of the wide spectrum of species it attracts relative to the sampling effort; Waring and Townsend, 2003), many moth species (micromoths in particular) are not attracted to light. This might explain why fewer micromoths than macromoths were collected in this study (i.e. relative to the total number of species found in the British Isles). However, our trapping method allowed us to detect general patterns in moth abundance/richness associated with woodland character, and contrast the responses of micro- vs. macromoth species, even if this does not reflect the habitat preferences of all moth species.

5. Conclusions

In summary, woodland vegetation character, woodland patch configuration and the surrounding landscape all influenced moth populations in farmland woodlands. Even though rarer species might require specific management actions to enhance their populations, the design and management of woodland patches within agricultural landscapes should take into consideration the following general points to ensure the creation/protection of habitat of high conservation value for moths:

1. Woodlands composed of a large number of tree species (and a high proportion of native species) support high moth abundance and species richness.
2. The presence of grazing stock in a woodland patch has strong negative effects on moth abundance and diversity.
3. Large woodland patches of compact shapes (with a large proportion of woodland core habitat), located close to other woodlands are associated with high moth abundance and species richness. Small woodland patches can potentially maintain a relatively high abundance and species richness of moths, but shape and proximity to other woodlands are of particular importance in these cases.
4. Moths are influenced by the surrounding woodland mostly at small spatial scales (within 500 m); however, macromoth 'woodland species' are influenced at larger (≤ 1500 m) spatial scales and are, therefore, likely to benefit from a wider landscape-scale management approach taking into consideration woodland cover within the landscape, habitat connectivity and the location of woodland patches with respect to other woodlands.

Acknowledgements

We wish to thank the landowners and Estate managers who granted us permission to conduct this study on their land, and R.

Dawson and R. Griffiths for their help with macromoth identification. Special thanks to K. Bland (National Museums of Scotland) for identifying micromoth specimens and to J. Minderman for his advice on statistical analyses. Thanks also to M. Usher and two anonymous reviewers for their valuable comments on this manuscript, to CONACYT for providing a graduate scholarship (189261) to E.F.M., and to Bat Conservation International, the British Ecological Society and the People's Trust for Endangered Species for their financial support.

Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2012.04.019>.

References

- Akaike, H., 1974. A new look at the statistical model identification. *IEEE Trans. Automat. Control* 19, 716–723.
- Anonymous, 2007. Lepidoptera on Forestry Commission Land in England; Conservation Strategy 2007–2017. Butterfly Conservation & Forestry Commission England.
- Blakesley, D., Buckley, P., 2010. *Managing Your Woodland for Wildlife*. Pisces Publications, Newbury.
- Bland, K., Young, M.R., 1996. Priorities for conserving Scottish moths. In: Rotheray, G.E., MacGowan, I. (Eds.), *Conserving Scottish Insects*. Edinburgh Entomological Club, Edinburgh, pp. 27–36.
- Bright, P.W., 1998. Behaviour of specialist species in habitat corridors: arboreal dormice avoid corridor gaps. *Anim. Behav.* 56, 1485–1490.
- Broome, A., Clarke, S., Peace, A., Parsons, M.S., 2011. The effect of coppice management on moth assemblages in an English woodland. *Biodivers. Conserv.* 80, 729–749.
- Conrad, K.F., Woiwod, I.P., Parsons, M., Fox, R., 2004. Long-term population trends in widespread British moths. *J. Insect Conserv.* 8, 119–136.
- Conrad, K.F., Warren, M.S., Fox, R., Parsons, M.S., Woiwod, I.P., 2006. Rapid declines of common, widespread British moths provide evidence of an insect biodiversity crisis. *Biol. Conserv.* 132, 279–291.
- Crabtree, J.R. (Ed.), 1996. *Evaluation of the Farm Woodland Premium Scheme – Economics and Policy Series No 1*. Macaulay Land Use Research Institute, Aberdeen.
- Crawley, M.J., 2007. *The R Book*. John Wiley & Sons, West Sussex.
- Debinski, D.M., Holt, R.D., 2000. A survey and overview of habitat fragmentation experiments. *Conserv. Biol.* 14, 342–355.
- Didham, R.K., Ghazoul, J., Stork, N.E., Davis, A.J., 1996. Insects in fragmented forests: a functional approach. *Trends Ecol. Evol.* 11, 255–260.
- Dolman, P.M., Hinsley, S.A., Bellamy, P.E., Watts, K., 2007. Woodland birds in patchy landscapes: the evidence base for strategic networks. *Ibis* 146, 146–160.
- EDINA Digimap Ordnance Survey Service. OS MasterMap Topography Layer. <<http://edina.ac.uk/digimap>> (accessed February 2010).
- EDINA Historic Digimap Service. Ordnance Survey County Series 1:10560, Published 1951. <<http://edina.ac.uk/digimap>> (accessed May 2010).
- Ekroos, J., Heliölä, J., Kuussaari, M., 2010. Homogenization of lepidopteran communities in intensively cultivated agricultural landscapes. *J. Appl. Ecol.* 47, 459–467.
- Emmet, A.M., Heath, J., 1991. *The Moths and Butterflies of Great Britain and Ireland*, vol. 7, Part 2. Harley Books, Essex.
- ESRI Inc., 2006. ArcGIS 9.2. <<http://www.esri.com>>.
- Ewers, R.M., Didham, R.K., 2008. Pervasive impact of large-scale edge effects on a beetle community. *Proc. Natl. Acad. Sci.* 105, 5426–5429.
- Ewers, R.M., Thorpe, S., Didham, R.K., 2007. Synergistic interactions between edge and area effects in a heavily fragmented landscape. *Ecology* 88, 96–106.
- Fitzgibbon, C.D., 1997. Small mammals in farm woodlands: the effects of habitat, isolation and surrounding land-use patterns. *J. Appl. Ecol.* 34, 530–539.
- Fox, R., Conrad, K.F., Parsons, M.S., Warren, M.S., Woiwod, I.P., 2006. *The State of Britain's Larger Moths*. Butterfly Conservation & Rothamsted Research, Dorset.
- Fuentes-Montemayor, E., Goulson, D., Park, K.J., 2011. 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, 532–543.
- Hammer, O., Harper, D.A.T., Ryan, P.D., 2001. PAST: paleontological statistics software for education and data analysis. *Paleontol. Electron.* 4, 9.
- Hinsley, S.A., Bellamy, P.E., Newton, I., Sparks, T.H., 1995. Habitat and landscape factors influencing the presence of individual breeding bird species in woodland fragments. *J. Avian Biol.* 26, 94–104.
- Jennings, N., Pocock, M.J.O., 2009. Relationships between sensitivity to agricultural intensification and ecological traits of insectivorous mammals and arthropods. *Conserv. Biol.* 23, 1195–1203.
- Kent, M., Coker, P., 1992. *Vegetation Description and Analysis: A Practical Approach*. John Wiley & Sons, Chichester.

- Kitching, R.L., Orr, A.G., Thalib, L., Mitchell, H., Hopkins, M.S., Graham, A.W., 2000. Moth assemblages as indicators of environmental quality in remnants of upland Australian rain forest. *J. Appl. Ecol.* 37, 284–297.
- Lee, M., Fahrig, L., Freemark, K., Currie, D.J., 2002. Importance of patch scale vs. landscape scale on selected forest birds. *Oikos* 96, 110–118.
- Littlewood, N.A., 2008. Grazing impacts on moth diversity and abundance on a Scottish upland estate. *Insect Conserv. Diversity* 1, 151–160.
- Magurran, A.E., 1988. *Ecological Diversity and Its Measurement*. Princeton University Press, New Jersey.
- Mason, W.L., 2007. Changes in the management of British forests between 1945 and 2000 and possible future trends. *Ibis* 149, 41–52.
- McGarigal, K., McComb, W.C., 1995. Relationships between landscape structure and breeding birds in the Oregon coast range. *Ecol. Monogr.* 65, 235–260.
- McGarigal, K., Cushman, S.A., Neel, M.C., Ene, E., 2002. FRAGSTATS: Spatial Pattern Analysis Program for Categorical Maps – University of Massachusetts. <www.umass.edu/landeco/research/fragstats/fragstats.html>.
- Merckx, T., Feber, R., 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.
- 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.
- Murcia, C., 1995. Edge effects in fragmented forests: implications for conservation. *Trends Ecol. Evol.* 10, 58–62.
- New, T.R., 2004. Moths (Insecta: Lepidoptera) and conservation: background and perspective. *J. Insect Conserv.* 8, 79–94.
- Nieminen, M., Rita, H., Uuvana, P., 1999. Body size and migration rate in moths. *Ecography* 22, 697–707.
- Proctor, M., Yeo, P., Lack, A., 1996. *The Natural History of Pollination*. Harper Collins, London.
- Quine, C.P., Watts, K., 2009. Successful de-fragmentation of woodland by planting in an agricultural landscape? An assessment based on landscape indicators. *J. Environ. Manage.* 90, 251–259.
- R Development Core Team, 2010. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Ricketts, T.H., Daily, G.C., Ehrlich, P.R., Fay, J.P., 2001. Countryside biogeography of moths in a fragmented landscape: biodiversity in native and agricultural habitats. *Conserv. Biol.* 15, 378–388.
- Schielzeth, H., 2010. Simple means to improve the interpretability of regression coefficients. *Methods Ecol. Evol.* 1, 103–113.
- Southwood, T.R.E., Henderson, P.A., 2000. *Ecological Methods*, third ed. Blackwell Science, Oxford.
- Stewart, G.B., Pullin, A.S., 2008. The relative importance of grazing stock type and grazing intensity for conservation of mesotrophic 'old meadow' pasture. *J. Nat. Conserv.* 16, 175–185.
- Summerville, K.S., Crist, T.O., 2001. Effects of experimental habitat fragmentation on patch use by butterflies and skippers (Lepidoptera). *Ecology* 82, 1360–1370.
- Summerville, K.S., Crist, T.O., 2002. Effects of timber harvest on forest Lepidoptera: community, guild, and species responses. *Ecol. Appl.* 12, 820–835.
- Summerville, K.S., Crist, T.O., 2003. Determinants of lepidopteran community composition and species diversity in eastern deciduous forests: roles of season, eco-region and patch size. *Oikos* 100, 134–148.
- Summerville, K.S., Crist, T.O., 2004. Contrasting effects of habitat quantity and quality on moth communities in fragmented landscapes. *Ecography* 27, 3–12.
- Summerville, K.S., Crist, T.O., 2008. Structure and conservation of lepidopteran communities in managed forests of northeastern North America: a review. *Can. Entomol.* 140, 475–494.
- Tscharntke, T., Steffan-Dewenter, I., Kruess, A., Thies, C., 2002. Characteristics of insect populations on habitat fragments: a mini review. *Ecol. Res.* 17, 229–239.
- Usher, M.B., Keiller, S.W.J., 1998. The macrolepidoptera of farm woodlands: determinants of diversity and community structure. *Biodivers. Conserv.* 7, 725–748.
- Usher, M.B., Brown, A.C., Bedford, S.E., 1992. Plant species richness in farm woodlands. *Forestry* 65, 1–13.
- Vaughan, N., 1997. The diets of British bats (Chiroptera). *Mammal Rev.* 27, 77–94.
- Waite, S., 2000. *Statistical Ecology in Practice: A Guide to Analysing Environmental and Ecological Field Data*. Prentice Hall, London.
- Waring, P., 1989. *Moth Conservation Project News Bulletin 2*. Nature Conservancy Council, Peterborough.
- Waring, P., Townsend, M., 2003. *Field Guide to the Moths of Great Britain and Ireland*. British Wildlife Publishing, Dorset.
- Watts, K., 2006. British forest landscapes: the legacy of fragmentation. *Q. J. Forest.* 100, 273–279.
- Wilson, J.D., Morris, A.J., Arroyo, B.E., Clark, S.C., Bradbury, R.B., 1999. A review of the abundance and diversity of invertebrate and plant foods of granivorous birds in northern Europe in relation to agricultural change. *Agric. Ecosyst. Environ.* 75, 13–30.
- Young, M., 1997. *The Natural History of Moths*. Poyser Natural History, London.
- Young, M.R., Barbour, D.A., 2004. Conserving the New Forest burnet moth (*Zygaena viciae*) in Scotland; responses to grazing reduction and consequent vegetation changes. *J. Insect Conserv.* 8, 137–148.
- Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. *Mixed Effects Models and Extensions in Ecology With R*. Springer Science+Business Media, New York.