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Title

Moth communities and agri-environment schemes: examining the effects of hedgerow cutting regime on diversity, abundance and parasitism.

Running title

Effects of hedgerow cutting on moth communities

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Abstract

1. Hedgerows provide an important habitat for wildlife including invertebrates, representing a large proportion of semi-natural habitat patches in the modern agricultural landscapes of the UK and Europe. Around 40% of hedgerow length in England is managed under agri-environment scheme (AES) options, which specify less frequent cutting and advise cutting in winter.
2. Hedgerow management can alter habitat structure and quality, potentially influencing invertebrate community structure. We assessed the impacts of management treatments on moth communities and their parasitoids. Two treatments ('cutting frequency': once every one, two or three years, and 'cutting time': autumn vs. winter) were applied to a long running hedgerow experiment to mimic AES prescriptions. Moth larvae were collected from the hedgerows, identified and reared to determine parasitism. Hedgerow structure and foliar quality were quantified and related to changes in moth abundance, diversity, species richness and parasitism.
3. Hedgerow management did not significantly affect overall abundance of moth larvae, but did affect the abundance of certain feeding guilds and trophic interactions with parasitoids. Concealed moth larvae (mining, tentiform and case-bearing) were more abundant on hedgerows cut infrequently (every 2 or 3 years vs. annually). Parasitism rates were higher on hedgerows cut less often, when these were cut in autumn. There was a strong trend towards greater moth species richness and diversity on winter cut hedgerows.

4. AES management can thus have complex effects on invertebrate communities. The abundance of some moths may be positively affected by AES hedgerow management and this can have knock-on effects on parasitoid abundance.

Keywords

Agri-environment schemes, Entry Level Stewardship, hedge cutting, Lepidoptera, moths, parasitism, plant architecture, rearing larvae

Introduction

Agricultural expansion and intensification of farming practices are recognised as major threats to biodiversity (e.g. Millennium Ecosystem Assessment, 2005; Butler *et al.*, 2007). During the 20th century, around 50% of the hedgerows in the UK were removed to facilitate mechanisation and increase agricultural productivity (Barr & Parr, 1994; Croxton *et al.* 2004). Today, hedgerows still form a major component of the agricultural landscape (Barr & Gillespie, 2000); a recent survey estimated the total length of managed hedgerows in Great Britain to be 477,000 km, with 402,000 km in England (Carey *et al.*, 2008). They support a diverse range of species and provide the most widespread semi-natural habitat in heavily human-dominated landscapes across England (Natural England, 2009). Hedgerows have been shown to be important for wildlife in terms of habitat connectivity (Dover & Fry, 2001; Merckx *et al.*, 2010; Slade *et al.*, 2013) and shelter provision (Merckx *et al.*, 2008).

Across Europe, agri-environment schemes (AES), which encourage the environmentally sensitive management of farmland, are one option being used to try to halt and potentially reverse biodiversity declines (Merckx *et al.*, 2012). Currently, 70% of farmland in England is managed under AES at an annual cost of over £400 million (Natural England, 2013a). The Entry Level Stewardship (ELS) scheme was introduced in 2005 as a non-competitive, widely adopted scheme whereby land owners and managers receive payment in return for maintaining or enhancing the biodiversity value of their land, or managing it in environmentally sensitive ways (Davey *et al.* 2010; Natural England, 2013a). The hedgerow management options under the AES ELS scheme are some of the most widely adopted, with over 40% of English hedgerows actively managed under the initiative (Natural England, 2009). There is a recognised lack of evidence for the benefits of AES to biodiversity (Kleijn

& Sutherland, 2003), particularly for cryptic, poorly monitored taxa. Such evidence will be important for justifying continued investment in AES on environmental grounds.

Hedgerows are managed to prevent them from becoming broken up and overgrown and to make them more dense and stock-proof (since 1998, losses of 31,000 km of British hedges have been associated largely with a lack of management; Carey *et al.*, 2008). Traditionally, this was achieved through labour-intensive cutting by hand (Turnbull, 2005). Today, annual post-harvest autumn flailing to maintain hedgerows is the most common management outside AES in England (Staley *et al.*, 2012). The English ELS scheme specifies less frequent cutting regimes, including bi- and triennial cutting (Natural England, 2013b), and recommends cutting in the following winter rather than post-harvest. Cutting less frequently can lead to denser hedgerows (Natural England, 2007) and increase fruit production by hedgerow plants by up to 40% compared with hedgerows cut annually (Staley *et al.*, 2012). This results in greater food availability for birds and small mammals. Winter cutting gives wildlife longer to capitalise on fruit and seeds and avoids disturbing the hedgerow and associated wildlife during the end of the bird breeding season (Natural England, 2007).

Hedgerow cutting causes changes in plant architecture which can be defined as the size, growth form and variety of the parts of a plant occurring above ground (Lawton, 1983). More architecturally complex plants (i.e. those with higher levels of branching complexity) have been shown to support higher levels of diversity (Leather, 1986; Araujo *et al.*, 2006), in particular, more herbivorous arthropods (Lawton, 1983; Alonso & Herrera, 1996; Borges & Brown, 2001; Lara *et al.*, 2008), than structurally simple ones. Changes in plant architecture can affect the success and distribution of natural enemies, such as predatory arthropods (Maudsley *et al.*, 2002) which have a role in natural pest control in agriculture (e.g. Dennis &

Fry, 1992). The searching efficiency of parasitoids has been shown to be sensitive to changes in architecture (Schoonhoven *et al.*, 2005). Gingras *et al.* (2002) showed that with increased levels of connectivity within a plant structure (i.e. a more complex plant), the search efficiency of ovipositing *Trichogramma* parasitoids was decreased compared with females searching for host eggs on structurally simple plants.

The relationships between architectural complexity and beetle assemblages (Woodcock *et al.*, 2007) and AES management and biological pest control provision (Olson & Wäckers, 2007) have been investigated in the context of field margin AES. However, the effect of hedgerow AES on parasitism rates has not yet been studied. The purpose of this study was to quantify the changes in moth larval abundance, species richness, diversity and parasitism rates caused by different hedgerow cutting regimes and to assess the extent to which these changes can be explained by changes in hedgerow architecture. We studied hawthorn (*Crataegus monogyna* Jacq.) dominated hedgerows which are typical throughout lowland England.

We used moths as a target group for this study as Lepidoptera are one of the largest insect groups with over 2,900 species in the UK (Bradley, 2000). Their larvae are important as herbivores, pollinators and as a food source for numerous animals including mammals, birds and other insect species (Scoble, 1995). Significant declines have been documented for many macro moth species in the UK and beyond, with a range of possible drivers including agricultural intensification (Fox, 2013; Fox *et al.*, 2013). Some micro moth species are also known to be under threat, as demonstrated by the listing of 25 species as Priority Species in the UK Biodiversity Action Plan since 2000 (Fox *et al.*, 2013). Most previous work looking at invertebrates in hedgerows has focussed on butterflies and crop pests (Maudsley, 2000) (which use hedges as nectar sources), rather than species that are directly trophically linked

with the hedgerows (i.e. the larvae develop on hedgerow plants themselves (but see Merckx & Berwaerts, 2010)). A recent study by Fuentes-Montemayor *et al.* (2011) examined the effectiveness of AES farmland management, including hedgerow cutting, on moth populations. Their study looked at the effects of cutting every three years under a Scottish AES compared with standard management on adult moths which were attracted using light traps, and found no benefit of AES hedgerow management on micro and macro-moth populations. The current study looks at the effects of AES ELS options (both cutting timing and frequency of cutting), as well as standard management, on the abundance and diversity of moth larvae with direct trophic links with the hedgerows.

We tested the following hypotheses:

- i) Moth larval abundance, species richness and diversity will be higher on hedgerows cut less frequently.
- ii) Hedgerows cut less frequently will have higher levels of structural complexity.
- iii) Hedgerows cut after autumn harvest (September) will have higher levels of moth larval abundance, species richness and diversity compared with those cut later in the season (January/February), as a consequence of winter cutting removing eggs laid on autumn growth.
- iv) Parasitism rate (proportion of parasitised individuals) will decrease with increasing hedgerow architectural complexity.

Materials and Methods

Experimental site

In 1961, three hawthorn hedgerows were planted for experimental purposes at Monks Wood field site, Cambridgeshire, England (for further details, see Croxton *et al.*, 2004; Staley *et al.*, 2012). Each hedge is orientated north-south, is 200 m in length and separated by at least 50 m. The surrounding vegetation is a relatively homogenous grass sward managed as an annual meadow. In 2005, sections of three hedgerows were divided into 32 contiguous plots, each 15 m long, and subjected to two treatments in a random factorial design: i) cutting frequency; annual, biennial and once every three years, and ii) the timing of cutting; post-harvest autumn (September) and winter (January/February). Each of the six treatment combinations was replicated either eight (for annually cut plots) or four times (for biennial and 3 year plots). Data collection was carried out when the cutting experiment had completed two full cycles; i.e. hedgerows cut every two or three years had two and three years growth on respectively and were due to be cut later in the same year. The end 3 m of each plot was not sampled to avoid edge effects.

Moth sampling and rearing

Larvae were collected at the beginning of May, June and July 2011. Two methods were used:

- i. Timed search: a 1 m x 0.5 m frame quadrat was attached to a range pole at a height of 1.5 m and set against the hedgerow at 5 and 10 m along the length of each plot. All moth larvae and mined leaves were collected from within the quadrat for three minutes.
- ii. Hedgerow beating: a 2 m section of plastic guttering was inserted through the hedgerow at 0.8 m height at two locations along each 15 m plot (avoiding 5 and 10 m where quadrat sampling occurred). The vegetation above was struck hard three times with a metal pole to dislodge larvae and loose foliar material which was collected (Maudsley *et al.*, 2002).

Empty leaf mines and exuviae (visible tracks where larvae have formed a ‘tunnel’ by consuming plant material from in between layers of the leaf tissue) were photographed for identification. Those identified to species level were included in subsequent analyses as individuals from each plot. Larvae were placed into labelled 2.5 cm diameter glass tubes with fresh foliage and stoppers with small air holes, and reared at ambient temperatures to pupation to determine levels of parasitism. All samples in the analyses which follow had emerged by the end of February 2012. Foliage was changed twice a week and the development of the larva monitored. Emerging parasites were stored in 70% Industrial Methylated Spirits. Adult moths were euthanized and identified to species level using Waring & Townsend (2009) and UK Moths (Kimber 2013) (if not determined at the larval stage). For analysis, moths were assigned to one of two functional feeding guilds: i) free-living, whereby the larvae spends most or all of its life cycle free roaming and feeding externally on the leaves, vs. concealed; ii) larvae which mine in the leaf tissue or form protective cases from foliar material (e.g. *Coleophora* spp., Coleophoridae). This grouping is a convenient means of assigning species to different guilds which are likely to be affected by plant chemistry and natural enemies in similar ways (Price *et al.*, 2011). Species from both guilds sampled in the study exhibit a variety of life histories. Most of the concealed species in this study fly in the summer and early autumn months, with some species capable of multiple generations (e.g. *Parornix* and *Phyllonorycter* spp., Gracillariidae). Some overwinter as pupae (e.g. *Phyllonorycter* spp.) within the leaf mine, while others (*Stigmella* spp., Nepticulidae) may leave the mine in order to pupate on the leaf surface. Others overwinter as larvae (*Coleophora* spp.), and pupate within their protective cases. Most of the free-living species studied also fly during the summer and autumn months, and overwinter at a variety of life stages.

Hedgerow architecture and resource availability measurements

Architectural parameters were measured in June. Hedgerow height and width were measured five times along each plot using a range pole held against the hedgerow face and by inserting the range pole through the hedgerow at a height of 0.8 m and measuring the widest point. The number, total biomass and mean biomass of leaves was calculated at three points on each plot (4, 8 and 12 m) using a 0.5 m x 0.25 m frame quadrat attached to a range pole. The quadrat was laid against the hedgerow and every leaf within the quadrat was removed and counted before drying for three days at 80°C. Samples were weighed and the mean biomass of a leaf was calculated. The areas along the plots where leaves had been removed were avoided on subsequent larvae collection visits to reduce the effects of defoliation on measured larval abundance.

To measure branching density and length, a 1 m x 0.5 m quadrat attached to a range pole at a height of 1.5 m was placed against the hedgerow face at two locations per plot and the number of protruding branches was counted. Within each quadrat, five branches were selected at random. We measured the length to which each branch extended from the hedgerow face and the number of its constituent parts (i.e. number of one/two/three year old growing tips and number of one/two year old thorn tips) as identified by nodes in the branches and changes in stem colouration. Sub-branching density was calculated by calculating the volume of space taken up by the main branches on each plot and determining the total number of sub-branches found within a hypothetical 10 x 10 x 10 cm cube.

Foliar quality analysis

Foliage nitrogen content is considered to be one of the major limiting factors to phytophagous insect population growth (Mattson, 1980), and has been shown to be strongly positively

linked with insect fecundity (Awmack & Leather, 2002), survival and adult size (e.g. Myers & Post, 1981). The concentration of carbohydrate in relation to protein (C:N) has been shown to be an important determinant of moth survivorship, egg size and growth rate (e.g. Colasurdo, Gélinas & Despland, 2009). The chemistry of hedgerow foliage is likely to be affected by hedgerow cutting; plant chemistry has been shown to vary in response to stress, as damage to foliage and branches can increase the breakdown and mobilisation of nitrogen (White, 1984). We therefore measured foliar carbon and nitrogen concentration to determine whether any relationships between moth abundance, species richness and diversity and cutting treatment were a result of foliar quality changes between the treatments. Three growing tips, thorn tips and leaf rosettes were collected from evenly spaced intervals along each plot during each of the three moth larvae sampling periods. Leaves were removed from the stems, and frozen within three hours, before freeze drying (Heto PowerDry PL3000) for at least 22 hours (condenser temperature $<-55^{\circ}\text{C}$, pressure $<0.3\text{ hPa}$). Dried leaf samples were then milled using a ball mill (Pulverisette 23, Fritsch GmbH, Germany) and the carbon and nitrogen concentration of the samples was determined using dry combustion, whereby a known sample weight of finely ground leaf material is burnt in oxygen and the carbon and nitrogen content of the original sample is determined from the resulting gases (Elementar Vario EL CHNS analyser, Elementar Analysensysteme GmbH, Germany (Bremner & Tabatabai, 1971)).

Statistical analyses

All statistical analyses were carried out in R (version 2.14.1 (R Development Core Team 2011)). Cutting frequency, cutting timing and the interaction between them were included as factors (for ANOVA) or fixed effects (for generalized linear mixed models (GLMM, package lme4; Bates, 2011) and mixed effect linear models (LME, package nlme; Pinheiro *et al.*,

2009)) in all initial models. Hedge was included as a blocking factor with plot nested within hedge in all ANOVA to account for any variation in the data due to the position of the experimental plot. For GLMM and LME, hedge was included as a fixed factor (due to having less than the recommended 5-6 levels for a random factor (Bolker *et al.*, 2009)), with plot as a random factor. All models were simplified where possible by testing the effects of dropping factors or interaction terms using likelihood ratio tests (Faraway, 2006). In addition, plant architecture and foliar quality variables were included as co-variables in the analyses of moth abundance, richness, diversity and parasitism. The significance of these co-variables was tested using likelihood ratio tests (Faraway, 2006). Once a model could not be simplified further without loss of explanatory power, residual plots were examined to check the fit of the data to the model (Faraway, 2006) and the model assessed for influential observations.

Moth abundance, species richness and diversity

The effects of cutting frequency and timing on total abundances of larvae and species richness (i.e. the total number of species occurring on each plot) were tested using GLMMs. Abundance was summed across both sampling methods (quadrat and hedge beating) for each plot in order to take into account any variation in the data due to the method of collection. A Poisson error structure was used to analyse the abundance and species richness data as both variables were count data. In addition, abundance was split by functional guild (free-living and concealed) and analysed in the same way. Shannon-Weaver species diversity indices were calculated (Burn, 2004) across both sampling methods for each plot at each time point, and the data analysed using LME modelling. For all analyses on abundance, species richness and diversity, sampling date was included as a fixed factor.

Parasitism

The effects of cutting frequency and timing on rate of parasitism were tested using a GLMM with binomial error structure, with parasitism coded as '1' (parasitised) and '0' (not parasitised) for each reared sample (excluding those from which neither moth nor parasite emerged, giving a total of 218 observations). The functional feeding guild from which the original larvae belonged was entered as an explanatory variable (free-living vs. concealed), along with the total abundance of larvae found on the plot (analogous to a measure of resource availability to searching parasitoids) and architectural parameters.

Architectural variables

The effect of hedge cutting frequency, timing and the interaction between them on each hedge architecture response variable was analysed using ANOVA. Hedgerow architecture variables (hedge height, hedge width, number of leaves, total leaf biomass, leaf size (average leaf biomass), number of branches and sub-branching density) were pooled per plot. Significant results were further investigated using post-hoc Tukey tests to determine differences between individual treatments.

Foliar quality

The effects of cutting frequency, cutting timing and the interaction between them on foliar nitrogen and carbon concentrations were tested using ANOVA. Both carbon and nitrogen data were log transformed in order to normalise the data. Sampling date was entered as a fixed effect.

Results

Moth larval abundance

A total of 865 larvae, leaf mines and exuviae were collected across the three sampling periods (745 of which were identified to species level, see Supplementary Materials). Of the samples reared, 218 emerged, comprising 79 parasites and 139 moths. All but one of the parasitoids (a Tachinid fly) were Hymenopterans. All larvae collected were moths (Heterocera); no butterfly (Rhopalocera) larvae were found. The moths which emerged belonged to 42 species (see Supplementary Materials), including leaf miners (mostly *Stigmella* spp.), case bearers (*Coleophora* spp.) and various free-living micro and macro-moth species. Overall mean larval abundance (all feeding guilds) and mean abundance of free-living larvae were not significantly affected by the frequency or timing of hedgerow cutting (GLMM likelihood ratio tests (LRTs): all guilds; frequency $\chi^2_1 = 1.577$, $p = 0.209$; timing $\chi^2_1 = 1.358$, $p = 0.244$; frequency: timing $\chi^2_1 = 3.210$, $p = 0.069$, free living; frequency $\chi^2_1 = 1.121$, $p = 0.290$; timing $\chi^2_1 = 0.096$, $p = 0.756$, frequency: timing $\chi^2_1 = 1.078$, $p = 0.299$). Total larval abundance showed a trend towards an interaction occurring between cutting and timing ($p = 0.069$); annually cut plots supported more larvae when cut in winter, whereas plots cut less frequently supported more when cut in autumn.

The abundance of concealed larvae was significantly greater on hedges cut less frequently than those cut annually (GLMM LRT: $\chi^2_2 = 8.884$, $p = 0.012$). This effect was only seen for hedgerows cut in autumn (GLMM LRT: $\chi^2_1 = 5.831$, $p = 0.016$; Figure 1). Overall, concealed larvae were more abundant on hedgerows cut in winter compared with those cut in autumn (GLMM LRT: $\chi^2_2 = 7.362$, $p = 0.025$), particularly so on annually cut hedgerows (Figure 1). None of the measured architecture variables or nitrogen concentration data explained the differences seen in concealed larvae abundance and so were removed from the model (GLMM LRTs, all $p > 0.05$).

Diversity and species richness

Moth species richness showed a strong trend towards greater richness in hedgerow plots cut in the winter compared to those cut in autumn. Species richness increased from an average of 3.021 (± 0.222) species on plots cut in the autumn to 3.750 (± 0.235) on those cut in the winter (GLMM LRT: timing $\chi^2_1 = 3.776$, $p = 0.052$). There was no significant effect of frequency of cutting on the moth species richness (GLMM LRTs: frequency $\chi^2_1 = 0.372$, $p = 0.542$; frequency: timing $\chi^2_1 = 0.055$, $p = 0.815$). Analysis of species diversity across the plots showed a non-significant trend towards higher levels of species diversity occurring in winter cut plots (LME LRT: timing likelihood ratio = 3.168, d.f. = 1, $p = 0.075$). Hedgerow cutting frequency did not have a significant effect on species diversity and there was no significant interaction between the two factors (LME LRTs: frequency likelihood ratio = 0.210, d.f. = 1, $p = 0.647$; frequency: timing likelihood ratio = 0.564, d.f. = 1, $p = 0.453$).

Parasitism

The proportion of parasitised larvae differed between feeding guilds - concealed larvae experienced significantly higher levels of parasitism than free living larvae (GLMM LRT: $\chi^2_1 = 12.755$, $p < 0.001$). Parasitism was also significantly higher in plots where higher numbers of larvae were collected (GLMM LRT: $\chi^2_1 = 6.323$, $p = 0.012$). Neither timing of cutting nor frequency of cutting significantly affected the proportion of parasitism in reared samples (GLMM LRTs: timing $\chi^2_1 = 1.869$, $p = 0.172$, frequency $\chi^2_1 = 0.8163$, $p = 0.366$). There was, however, an interaction between timing and frequency of cutting (GLMM LRT: frequency: timing $\chi^2_1 = 5.250$, $p = 0.022$), where parasitism levels were higher on autumn cut plots when cut biennially or triennially compared with annually cut plots. Conversely, the highest level of parasitism in winter-cut plots occurred on those cut annually (Figure 2).

Parasitism rates were not explained by the measured architecture variables (GLMM LRTs, all $p > 0.05$).

Hedgerow architecture and resource availability

Hedgerows cut either biennially or triennially had significantly higher sub-branching densities than hedgerows cut every year (see Table 1 for ANOVA results). Plots cut every year had significantly more protruding branches on average, and fewer leaves than those cut less frequently (Tukey, $p < 0.05$). Hedgerows cut annually had heavier leaves than those collected from plots cut less frequently, and were significantly wider and taller (Table 1 Tukey, $p < 0.05$).

Cutting timing did not significantly affect sub-branching density or hedgerow width. Hedgerows cut in autumn were significantly shorter and also had significantly more protruding branches compared with those cut in winter (Tukey, $p < 0.05$). Hedgerows cut in autumn had significantly more leaves than hedgerows cut in winter, across all cutting frequency treatments (Tukey, $p < 0.05$). Hedgerows cut in winter had heavier leaves than those cut in autumn (Tukey, $p < 0.05$).

The total weight of leaves collected from the different hedgerows from an equal area did not differ significantly between cutting frequency or timing treatments. Leaves from annually autumn cut plots had a lower mean weight than those from plots cut annually in winter, whereas in plots cut once every three years, autumn cut plots had higher mean leaf weights. For biennially cut plots, mean leaf weights were similar regardless of cutting timing (Figure 3).

Foliar quality

Nitrogen concentration differed significantly between the periods sampled (ANOVA, $F_{(1, 89)} = 71.632, p < 0.001$), with samples collected in May having higher nitrogen concentrations than those collected in June and July. Plots cut less often had significantly lower concentrations of nitrogen in the tissues sampled than those cut annually (ANOVA, $F_{(1, 89)} = 24.258, p < 0.001$, annually cut average of $1.754\% \text{ N} \pm 0.031$, biennially/triennially cut average of $1.601\% \text{ N} \pm 0.028$). Cutting timing did not have a significant effect on nitrogen concentration (ANOVA, $F_{(1, 89)} = 0.994, p = 0.321$). The carbon concentration of tissues from plots cut less frequently was significantly higher than from those cut every year (ANOVA, $F_{(1, 89)} = 21.528, p < 0.001$). Sampling period and timing of cutting had no significant effect on foliar carbon concentration (ANOVA, $p > 0.05$).

Discussion

Management affects hedgerow architecture and foliar quality

Hedgerow cutting frequency had a significant and measurable effect on hedgerow architecture. As hypothesised, less frequently cut hedgerows had a higher sub-branching density, resulting in a more complex branching structure. This was true despite annually cut hedgerows having significantly more protruding branches than those cut less frequently; this could be as a result of the plants producing many short growing tips in reaction to cutting which do not get a chance to mature and produce side branches before cutting in the following year. The hedgerows cut less frequently did have significantly more leaves in this study, as the plants are left to grow for longer between cuts, and so are able to produce more leaves from a greater length and number of branches and shoots. Contrary to the expectation that plots cut less often would also contain a higher biomass of leaves (as a result of a greater

number of leaves), the total biomass of leaves did not vary between plots; hedgerows cut annually had fewer, larger (heavier) leaves. This could be the result of increased investment in fewer leaves by the hawthorn plants in frequently cut plots in order to maximise photosynthetic output. Thus, the total leaf resource available to moth larvae did not differ with cutting frequency or timing.

Hedgerow plots cut annually had a greater concentration of foliar nitrogen compared with those cut less frequently, as expected. Plants that are stressed, including those that are regularly defoliated by herbivores or mechanical damage, often have higher foliar nitrogen concentrations (Mattson, 1980; White, 1984). Leaves on annually trimmed hedges appear to offer a larger resource of higher quality (greater nitrogen content) to concealed moth larvae, which are relatively immobile and often feed on just one or a few leaves close to where they hatched from eggs. However, a greater number of concealed larvae were found on plots that were cut less frequently, suggesting female moths might be choosing to lay eggs in less frequently cut hedgerows. This may be due to other host plant quality factors that we did not investigate, such as phenolic or tannin content of the leaves. Alternatively, the lower number of concealed larvae on more frequently cut hedgerows could be the result of physical removal of eggs and larvae from these plots during cutting.

Architecture does not affect moth abundance or parasitism

The measured architectural variables did not significantly explain any of the observed patterns in moth larvae and parasitoid abundance. This finding is unexpected; other studies have shown a positive effect of increased architectural complexity on both invertebrate diversity and abundance (e.g. Leather, 1986; Borges & Brown, 2001; Araujo *et al.*, 2006; Lara *et al.*, 2008). Ovipositing female moths and parasitoids may be discriminating between

hedgerows based on characteristics which were not measured here, such as olfactory stimuli or aspects of foliar quality such as phenolic content (Visser, 1986).

Hedgerow management affects moth larval communities

The finding that abundance across all moth species did not significantly differ between cutting regimes is consistent with those of a study by Fuentes-Montemayor *et al.* (2011) in which the total abundance of moths did not differ between AES managed hedgerows and conventionally managed hedgerows (i.e. more frequently cut). Fuentes-Montemayor *et al.* (2011) divided their species into macro and micro-moths, but not by feeding strategy (concealed vs. free); our study illustrates the potential importance of grouping invertebrates by functional group.

Hedgerows managed under AES (ELS) recommendations (i.e. cut less often) supported significantly higher numbers of concealed moth larvae than hedgerows under a standard annual autumn cutting regime. This finding largely confirms our first hypothesis - that moth larval abundance and diversity will be inversely proportional to hedgerow cutting frequency - though the positive effect of less frequent cutting regimes on moth abundance was restricted to concealed species on autumn cut hedgerows. Both linear and tentiform mining species are very restricted in their location on a plant, with many only leaving the leaf mine upon pupation (although some species can move between mines as larvae (Connor & Taverner, 1997)). This implies that, for concealed species, female moths are selecting less frequently cut plots for oviposition, or that eggs may be physically removed from the hedgerow during cutting. In contrast, the abundance of free-living, more mobile, species did not increase in response to reduced hedgerow cutting; free-living larvae could have moved within and between hedgerow plots, making any abundance changes in relation to cutting regimes harder

to detect. Further investigation into the effects of cutting regimes on highly mobile taxa using spatially independent hedges under the different management regimes across a wider geographical area could confirm our conclusion that free-living larvae abundance is not affected by hedge cutting regime, or detect similar benefits as those found for less mobile concealed species.

We predicted that winter cutting would negatively affect moth abundance and diversity by removing eggs laid on autumn growth (hypothesis iii), as suggested in a publication by Natural England (2007). Many of the moth species collected in this study lay their eggs prior to both the autumn and the winter cutting dates, which may be why moth abundance was mostly unaffected by the timing of cutting. Indeed, contrary to our hypothesis, hedgerows cut in the winter showed a trend towards supporting a higher species richness and diversity of moths, showing a potential benefit of cutting hedgerows in winter rather than the autumn. Winter cut hedgerows also supported significantly more concealed larvae overall, particularly so for annually cut hedgerows. One reason for this could perhaps be that autumn cutting disturbs larvae whilst they are still feeding, or disturbs diapause sites. Whereas, winter cutting may occur after leaf fall, when overwintering moths are relatively safe from disturbance in the leaf litter. Therefore, the winter cutting recommended by AES prescriptions may offer benefits to certain moth species as well as nesting birds and other wildlife which feed on these, even under annual cutting regimes.

Cutting in autumn rather than winter may be beneficial for species which may still be active and ovipositing after the autumn cutting period, overwintering as immobile eggs on the outermost vegetation, such as the Brown Hairstreak butterfly (*Thecla betulae* L.) (Merckx & Berwaerts, 2010), which is not found at our study site.

The benefits of reduced cutting on moth abundance and diversity did not significantly differ between biennial regimes and those where hedgerows were cut every three years. Cutting every three years, whilst potentially benefiting other wildlife (Staley *et al.*, 2012), seems unlikely to convey extra benefits to certain groups of moth species (but see Merckx & Berwaerts, 2010). Further studies across broader geographical ranges and on larger, multi-species hedgerows will be needed to ascertain whether the results of this study are more broadly applicable. Nevertheless, it is worth noting that approximately half of all the hedgerows in the UK are pure hawthorn or hawthorn dominated (Cummins & French, 1994), making our results potentially widely relevant.

Parasitism of moth larvae is altered by hedgerow management regime

We found that parasitism levels were increased on less frequently cut, and therefore more structurally complex, hedgerows (when they were cut in autumn), contrary to the findings in a paper by Gingras *et al.* (2002) where parasitoid search efficiency decreased with increasing levels of structural complexity. This disproves our fourth hypothesis, that parasitism rate would be negatively related to architectural complexity, though it is consistent with findings in a meta-analysis by Langellotto & Denno (2004) which found that enhanced levels of structural complexity resulted in significant increases in the numbers of natural enemies (including parasitoids). Lara *et al.* (2008) found that parasitism was not directly related to architectural variables such as sub-branching density, as found in this study. The parasitoids examined in this study were all highly-mobile, flying parasitoid wasps (and one Tachinid fly). Architectural variables may be more important for less mobile natural enemies, such as beetles and spiders, particularly given the need for complex architecture for web-building spiders (Maudsley *et al.*, 2002). Parasitic wasps have been shown to respond to volatile

chemicals released by plants experiencing herbivore damage (Whitman & Eller, 1990); higher numbers of concealed larvae on less frequently autumn cut hedgerows may have attracted higher numbers of highly mobile flying parasitoids. Hedgerow cutting was found to have a significant effect on parasitism rates even after larval abundance and functional feeding guild were taken into consideration. This suggests that the effects of hedgerow cutting may be affecting parasitoids through architectural variables not measured in this study, changes in microclimate or changes to other factors not considered here such as olfactory stimuli.

Summary

Hedgerow architecture was significantly influenced by the different cutting regimes. The abundance of concealed moth larvae was affected positively by reducing hedgerow cutting frequency. In addition, moth species richness and diversity showed strong trends towards greater values on hedgerow plots cut in winter, rather than autumn. Parasitism levels increased on hedgerows cut less frequently (when cut in autumn), but this effect was not a result of the measured changes in architecture. This study demonstrates that less frequent hedgerow cutting, or winter vs. autumn cutting, as supported by English AES prescriptions, could have the potential to benefit the abundance of certain moths and their parasitoids. AES recommendations of winter cutting may also have the potential to benefit moth species richness and diversity. This finding, along with the benefits reported for other groups such as birds, provide further evidence for the justification of AES management on the ground of proven benefits to wildlife.

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References

- Alonso, C. & Herrera, C.M. (1996) Variation in herbivory within and among plants of *Daphne laureola* (Thymelaeaceae): correlation with plant size and architecture. *Journal of Ecology*, **84**, 495–502.
- Araujo, A.P.A., De Paula, J.D., Carneiro, M.A.A. & Schoereder, J.H. (2006) Effects of host plant architecture on colonization by galling insects. *Austral Ecology*, **31**, 343–348.
- Awmack, C.S. & Leather, S.R. (2002) Host plant quality and fecundity in herbivorous insects. *Annual Review of Entomology*, **47**, 817–844.
- Barr, C.J. & Gillespie, M.K. (2000) Estimating hedgerow length and pattern characteristics in Great Britain using Countryside Survey data. *Journal of Environmental Management*, **60**, 23–32.
- Barr, C.J. & Parr, T.W. (1994) Hedgerows: linking ecological research and countryside policy. In: Watt, T.A. & Buckley, G.P., (editors). *Hedgerow Management and Nature Conservation*. Wye College Press, London, pp. 119–136.
- Bates, D. (2011) Mixed models in R using the lme4 package. *Development*, **88**.
- Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H. & White, J.-S.S. (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution*, **24**, 127–135.
- Borges, P.A.V. & Brown, V.K. (2001) Phytophagous insects and web-building spiders in relation to pasture vegetation complexity. *Ecography*, **24**, 68–82.
- Bradley, J.D. (2000). *Checklist of Lepidoptera Recorded from the British Isles*. Second Edition (Revised). Bradley & Bradley, Fordingbridge.

551 Bremner, J.M. & Tabatabai, M.A. (1971) Use of automated combustion techniques for
552 total carbon, total nitrogen, and total sulfur analysis of soils. In: Walsh, L.M., editor.
553 *Instrumental Methods for Analysis of Soils and Plant Tissue*. Special Publication
554 Series, No. 2, Part 3, pp. 1–15. Soil Science Society of America, Madison.

555 Burn R.W. (2004) Shannon Diversity Index MS Excel Add-in. Accessed online at
556 <http://www.reading.ac.uk/ssc/software/diversity/diversity.html>

557 Butler, S.J., Vickery, J.A. & Norris, K. (2007) Farmland biodiversity and the footprint of
558 agriculture. *Science*, **315**, 381–384.

559 Carey, P.D., Wallis, S., Chamberlain, P.M., Cooper, A., Emmett, B.A., Maskell, L.C.,
560 McCann, T., Murphy, J., Norton, L.R., Reynolds, B., Scott, W.A., Simpson, I.C., Smart,
561 S.M., Ulliyett, J.M. (2008) *Countryside Survey: UK Results from 2007*. NERC/Centre for
562 Ecology & Hydrology, UK (CEH Project Number: C03259)

563 Colasurdo, N., Gélinas, Y. & Despland, E. (2009) Larval nutrition affects life history traits in
564 a capital breeding moth. *Journal of Experimental Biology*, **212**, 1794–1800.

565 Connor, E.F. & Taverner, M.P. (1997) The evolution and adaptive significance of the leaf-
566 mining habit. *Oikos*, **79**, 6–25.

567 Croxton, P.J., Franssen, W., Myhill, D.G. & Sparks, T.H. (2004) The restoration of neglected
568 hedges: a comparison of management treatments. *Biological Conservation*, **117**, 19–23.

569 Cummins, R.P. & French, D.D. (1994) Floristic diversity, management and associated land
570 use in British hedgerows. In: Watt, T.A., Buckley, G.P., (editors). *Hedgerow*
571 *Management and Nature Conservation*. Wye College Press, London. pp.95–106.

- 572 Davey, C.M. Vickery, J.A., Boatman, N., Chamberlain, D., Parry, H. & Siriwardena, G.M.
573 (2010) Regional variation in the efficacy of entry level stewardship in England.
574 *Agriculture, Ecosystems & Environment*, **139**, 121–128.
- 575 Dennis, P. & Fry, G.L.A. (1992) Field margins: can they enhance natural enemy population
576 densities and general arthropod diversity on farmland? *Agriculture, Ecosystems and*
577 *Environment*, **40**, 95–115.
- 578 Dover, J.W. & Fry, G.L.A. (2001) Experimental simulation of some visual and physical
579 components of a hedge and the effects on butterfly behaviour in an agricultural
580 landscape. *Entomologia Experimentalis et Applicata*, **100**, 221–233.
- 581 Faraway, J.J. (2006) *Extending the Linear Model with R: Generalized Linear, Mixed Effects*
582 *and Nonparametric Regression Models* (editors Carlin, B.P., Chatfield, C., Tanner, M. &
583 Zidek, J.). Chapman & Hall/CRC Press.
- 584 Fox, R. (2013) The decline of moths in Great Britain: a review of possible causes. *Insect*
585 *Conservation & Diversity*, **6**, 5–19.
- 586 Fox, R., Parsons, M.S., Chapman, J.W., Woiwod, I.P., Warren, M.S. & Brooks, D.R. (2013)
587 *The State of Britain's Larger Moths 2013*. Butterfly Conservation and Rothamsted
588 Research, Wareham, Dorset, UK
- 589 Fuentes-Montemayor, E., Goulson, D. & Park, K.J. (2011) The effectiveness of agri-
590 environment schemes for the conservation of farmland moths: assessing the importance
591 of a landscape-scale management approach. *Journal of Applied Ecology*, **48**, 532–542.
- 592 Gingras, D., Dutilleul, P. & Boivin, G. (2002) Modeling the impact of plant structure on host-
593 finding behavior of parasitoids. *Oecologia*, **130**, 396–402.

594 Kimber, I. (2013) UK Moths – your guide to the moths of Great Britain and Ireland.
 595 <http://ukmoths.org.uk>.

596 Kleijn, D. & Sutherland, W.J. (2003) How effective are European agri-environment schemes
 597 in conserving and promoting biodiversity? *Journal of Applied Ecology*, **40**, 947–969.

598 Langellotto, G.A. & Denno, R.F. (2004) Responses of invertebrate natural enemies to
 599 complex-structured habitats: a meta-analytical synthesis. *Oecologia*, **139**, 1–10.

600 Lara, D.P., Oliveira, L.A., Azevedo, I.F.P., Xavier, M.F., Silveira, F.A.O., Antonio, M.,
 601 Carneiro, A. & Fernandes, G.W. (2008) Relationships between host plant architecture
 602 and gall abundance and survival. *Revista Brasileira de Entomologia*, **52**, 78–81.

603 Lawton, J.H. (1983) Plant architecture and the diversity of phytophagous insects. *Annual*
 604 *Review of Entomology*, **28**, 23–39.

605 Leather, S.R. (1986) Insect species richness of the British Rosaceae: the importance of host
 606 range, plant architecture, age of establishment, taxonomic isolation and species-area
 607 relationships. *Journal of Animal Ecology*, **55**, 841–860.

608 Mattson, W.J. (1980) Herbivory in relation to plant nitrogen content. *Annual Review of*
 609 *Ecology and Systematics*, **11**, 119–161.

610 Maudsley, M. (2000) A review of the ecology and conservation of hedgerow invertebrates in
 611 Britain. *Journal of Environmental Management*, **60**, 65–76.

612 Maudsley, M., Seeley, B. & Lewis, O. (2002) Spatial distribution patterns of predatory
 613 arthropods within an English hedgerow in early winter in relation to habitat variables.
 614 *Agriculture, Ecosystems & Environment*, **89**, 77–89.

615 Merckx, T., Van Dongen, S., Matthysen, E., & Van Dyck, H. (2008) Thermal flight budget of
616 a woodland butterfly in woodland versus agricultural landscapes: An experimental
617 assessment. *Basic and Applied Ecology*, **9**, 433–442.

618 Merckx, T. & Berwaerts, K. (2010) What type of hedgerows do Brown hairstreak (*Thecla*
619 *betulae* L.) butterflies prefer? Implications for European agricultural landscape
620 conservation. *Insect Conservation and Diversity*, **3**, 194–204.

621 Merckx, T., Feber, R.E., Mclaughlan, C., Bourn, N.A.D., Parsons, M.S., Townsend, M.C.,
622 Riordan, P. & Macdonald, D.W. (2010) Shelter benefits less mobile moth species: The
623 field-scale effect of hedgerow trees. *Agriculture, Ecosystems & Environment*, **138**, 147-
624 151.

625 Merckx, T., Marini, L., Feber, R.E. & Macdonald, D.W. (2012) Hedgerow trees and
626 extended-width field margins enhance macro-moth diversity: implications for
627 management. *Journal of Applied Ecology*, **49**, 1396–1404.

628 Millennium Ecosystem Assessment (2005) *Ecosystems and human well-being*. Vol. 5. Island
629 Press, Washington, DC.

630 Myers, J.H. & Post, B.J. (1981) Plant nitrogen and fluctuations of insect populations: a test
631 with the cinnabar moth-tansy ragwort system. *Oecologia*, **48**, 151–156.

632 Natural England (2007) Hedge cutting : answers to 18 common questions. Available:
633 <http://naturalengland.etraderstores.com/NaturalEnglandShop/NE36>.

634 Natural England (2009) Agri-environment schemes in England 2009. DEFRA, UK.

635 Natural England (2013a) ‘*Area covered by Stewardship hits record high*’ Natural England
636 Press Release http://www.naturalengland.org.uk/about_us/news/2013/300113.aspx 30th
637 January 2013.

638 Natural England (2013b) Entry Level Stewardship – Environmental Stewardship Handbook.
639 DEFRA, UK, fourth edition.

640 Olson, D.M. & Wäckers, F.L. (2007) Management of field margins to maximize multiple
641 ecological services. *Journal of Applied Ecology*, **44**, 13–21.

642 Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & Team, t.R.C. (2009) nlme: Linear and
643 Nonlinear Mixed Effects Models. R package.

644 Price P.W., Denno F.D., Eubanks M.D., Finke D.L. & Kaplan I. (2011) *Insect Ecology:*
645 *Behaviour, Populations and Communities*. Cambridge University Press, Cambridge, UK.

646 R Development Core Team (2011) R: A Language and Environment for Statistical
647 Computing (ed RDC Team). *R Foundation for Statistical Computing*, **1**, 409.

648 Schoonhoven, L.M., Van Loon, J.J.A. & Dicke, M. (2005) *Insect-plant Biology*. Oxford
649 University Press, Oxford, UK.

650 Scoble, M.J. (1995) *The Lepidoptera: Form, Function and Diversity*. Oxford University
651 Press, Oxford, UK.

652 Slade, E.M., Merckx, T., Riutta, T., Bebbier, D.P., Redhead, D., Riordan, P. & Whyte
653 Macdonald, D. (2013) Life-history traits and landscape characteristics predict macro-
654 moth responses to forest fragmentation. *Ecology*, **94**, 1519–1530.

655 Staley, J.T., Sparks, T.H., Croxton, P.J., Baldock, K.C.R., Heard, M.S., Hulmes, S., Hulmes,
656 L., Peyton, J., Amy, S.R. & Pywell, R.F. (2012) Long-term effects of hedgerow

657 management policies on resource provision for wildlife. *Biological Conservation*, **145**,
658 24–29.

659 Turnbull, C.G.N. (2005) *Shoot architecture II Control of branching. Plant architecture and*
660 *its manipulation*. Annual Plant Reviews (editor Turnbull, C.G.N.), pp. 92-120. Blackwell
661 Publishing (CRC Press).

662 Visser, J. H. (1986) Host odor perception in phytophagous insects. *Annual Review of*
663 *Entomology*, **31**, 121–144.

664 Waring, P. & Townsend, M. (2009) *Field Guide to the Moths of Great Britain and Ireland*.
665 British Wildlife Publishing, UK.

666 White, T.C.R. (1984) The abundance of invertebrate herbivores in relation to the availability
667 of nitrogen in stressed food plants. *Oecologia*, **63**, 90–105.

668 Whitman, D.W. & Eller, F.J. (1990) Parasitic wasps orient to green leaf volatiles.
669 *Chemoecology*, **1**, 69–76.

670 Woodcock, B.A., Potts, S.G., Pilgrim, E., Ramsay, A.J., Tscheulin, T., Parkinson, A., Smith,
671 R.E.N., Gundrey, A.L., Brown, V.K. & Tallowin, J.R. (2007) The potential of grass field
672 margin management for enhancing beetle diversity in intensive livestock farms. *Journal*
673 *of Applied Ecology*, **44**, 60–69.

674

Figure legends

Fig. 1. The mean number (\pm SE) of concealed larvae sampled (quadrats and hedge beating) from 15 m hedgerow plots over the three sampling periods, 1 = annually cut hedgerows, 2 = hedgerows cut once in two years, 3 = hedgerows cut once in three years. * = significant factor at $p < 0.05$. The statistical analysis of these data was conducted using a generalized linear mixed model with a Poisson error structure (see Methods). The error bars give an approximate indication of which treatments differ, but cannot be interpreted in the same way as for normally distributed data.

Fig. 2. The proportion of reared larvae experiencing parasitism from hedgerows receiving different cutting frequency treatments (1; annual, 2; biennial, 3; cut once every three years). * = significant factor at $p < 0.05$.

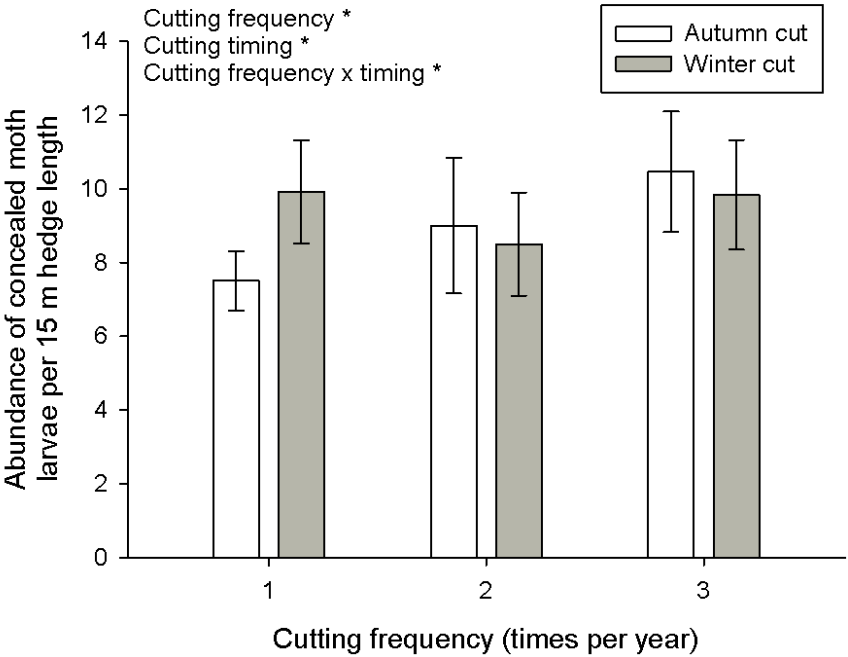
Fig. 3. The mean individual weight (\pm SE) of leaves sampled from quadrats on the hedgerow plots, 1 = annually cut hedgerows, 2 = hedgerows cut once in two years, 3 = hedgerows cut once in three years. *** = significant factor at $p < 0.001$.

Tables

Table 1. Results from Two-Way ANOVAs on hedgerow architecture parameters. *p* values highlighted in bold denote significance at the 0.05 level or below. Where interactions between the two hedgerow cutting factors were not found to be significant, these results are not shown.

706				
Factor	F	d.f.	P	
<i>Width</i>				
Cutting frequency	86.549	2, 23	< 0.001	
Timing	1.558	1, 23	0.224	
<i>Height</i>				
Cutting frequency	150.846	2, 23	< 0.001	
Timing	7.662	1, 23	0.011	
<i>Number of leaves</i>				
Cutting frequency	15.381	2, 23	< 0.001	
Timing	5.173	1, 23	0.0326	
<i>Total leaf weight</i>				
Cutting frequency	2.246	2, 23	0.129	
Timing	0.842	1, 23	0.368	
<i>Mean leaf weight</i>				
Cutting frequency	95.15	2, 21	< 0.001	
Timing	24.72	1, 21	< 0.001	
Timing x frequency	15.27	2, 21	< 0.001	
<i>Sub-branching density</i>				
Cutting frequency	38.289	2, 23	< 0.001	
Timing	0.021	1, 23	0.885	
<i>Number of branches</i>				
Cutting frequency	16.131	2, 23	< 0.001	
Timing	5.559	1, 23	0.0273	
724				

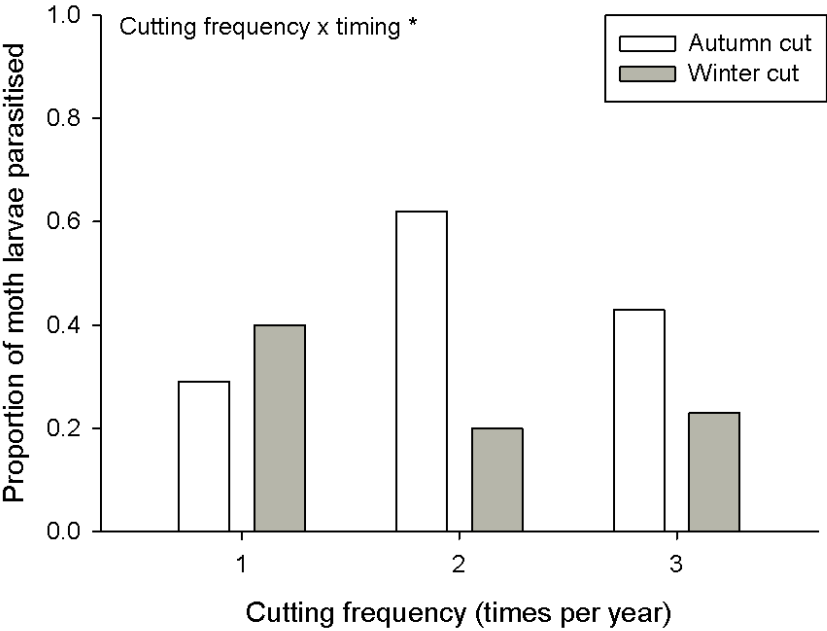
726 Figure 1



727

728

729 Figure 2



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