Landscape woody features, meadow plant composition and mowing regime shape moth communities in extensively managed grasslands

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Abstract

1. Agricultural intensification during the second half of the twentieth century, notably the degradation and progressive isolation of semi-natural grasslands, has led to a dramatic impoverishment of biodiversity over wide areas. Moths are not an exception and rapid declines of common and widespread species have been reported. Because moths are highly diverse in body size, mobility and habitat requirements, it is still not clear which, and at what scales, conservation measures should be applied to restore and conserve their populations.

2. We investigated how much of the variation in moth assemblages inhabiting extensively managed meadows is explained by the surrounding woody landscape features, grassland management and plant composition, and which specific variables are the most influential. Moths were sampled using light traps in 47 meadows distributed across the Swiss Plateau, a lowland region of intensive agriculture.

3. Results show that woody landscape features (hedgerows and forests), followed by grassland management and plant composition of the meadow itself are important predictors of moth abundance and species richness. Surrounding woody structures, such as percentage of forest as well as length of hedges within a 250 m radius were especially important for forest macromoths, explaining up to 51% of their abundance and 46% of species richness, whereas grassland management and plant composition played only marginal roles (≤ 15% each). Openland macromoths were ca equally influenced by woody landscape features and grassland management, which explained, respectively, 7 and 3% of their abundance, and 8 and 15% of their species richness. In contrast, micromoth abundance was more influenced by grassland management, notably the date of the first cut, and plant composition, which each explained 5% of the variation, whereas woody landscape features explained nothing.

4. Altogether, these results demonstrate the importance of woody features in the agricultural landscape and of biodiversity-friendly grassland management for the maintenance of integral

moth communities. Yet, effects vary between moth guilds, depending on their ecology and/or mobility.

Keywords: agriculture, agri-environment scheme, biodiversity, grassland, hedges, landscape, Lepidoptera, moths

Introduction

In the last decades, intensification of agricultural practices have led to today's spatially and temporally simplified landscape matrix found over most western European lowlands (e.g. Henle et al., 2008; Stoate et al., 2009). Semi-natural grasslands in these regions have become rare and isolated and often harbour impoverished plant, bird and invertebrate communities (e.g. Poschlod & WallisDeVries, 2002; Wesche et al., 2012). Concerns about the impacts of agricultural intensification on farmland bird populations has started decades ago (e.g. Carson, 1962), nonetheless populations continue to decline nowadays (e.g. Donald et al., 2006). The negative impact of modern management practices on invertebrates has also been widely reported (e.g. Benton et al., 2002); for example on diurnal butterflies (e.g. Van Dyck et al., 2009; Wenzel et al., 2006), but also on their related but far less investigated group, the moths (Fox, 2013; Fox et al., 2014). Rapid declines, at least as great as those for butterflies and birds, of still common and widespread moth species are now observed in Europe (Conrad et al., 2006; Groenendijk & Ellis, 2011). Among endangered moth species, the ones that live in open-canopy forests and grasslands are overrepresented (Pavlikova & Konvicka, 2012). It has been argued that because moths are holometabolous insects and experience non-, low- as well as mobile stages, with each stage depending on specific resources, small alterations in the quality or quantity of their habitats can have drastic negative effects on their populations (e.g. Jonason et al., 2013; Kadlec et al., 2009; Taylor & Morecroft, 2009).

To counter the loss in farmland biodiversity and to promote semi-natural habitats in general, agri-environment schemes (AES) were introduced in Europe in the mid-1980s and early-1990s (Kleijn & Sutherland, 2003). While the effectiveness of AES in promoting invertebrate biodiversity has been questioned (Kleijn et al., 2006), it has been shown that if well targeted some of these schemes can benefit moths. For example it has been demonstrated that extended-width field margins (minimum 6 m; current AES option in Oxfordshire, UK) locally increases species richness, but not abundance, of macromoths (Merckx et al., 2012),

57 and that in Scotland the species richness of micro- and macromoths as well as the abundance
58 of micromoths were significantly higher in grasslands under AES management compared to
59 conventionally managed grasslands (Fuentes-Montemayor et al., 2011; see also Taylor &
60 Morecroft, 2009). Furthermore Fuentes-Montemayor et al. (2011) found that the percentage
61 cover of surrounding semi-natural elements not declared as AES, such as rough grasslands
62 and scrubs, was an important landscape predictor for both macro- and micromoth abundance
63 and macromoth species richness, and Merckx et al. (2012) showed similar positive effects if
64 hedgerow trees were present. In summary, moth abundance and species richness are higher in
65 AES grassland elements compared to their conventionally counterparts, but are still strongly
66 influenced by the surrounding environment. Though, the relative contribution of all these
67 factors, as well as the local herbaceous plant composition is still unclear and requires further
68 research to improve conservation and restoration measures for farmland moths.
69 The aim of this study was to quantify and compare the effects of the surrounding
70 woody landscape features, the grassland management and vegetation composition of AES
71 grasslands on macromoth abundance and species richness, and micromoth abundance.
72 Extensively managed meadows are the most common AES type in Switzerland (representing
73 52% of all AES) and have recently been recognized as the best conservation instruments from
74 both green and sustainable points of view of the European Common Agricultural Policy
75 (Mouysset, 2014). Thus it is within this type of scheme that there is the highest long-term
76 conservation potential.
77 We hypothesized that a large proportion of the variation (r^2) observed in macromoth
78 abundance and species richness would be explained by surrounding woody landscape features
79 such as the amount of hedgerows and forest (Merckx et al., 2010; Merckx et al., 2012;
80 Ricketts et al., 2001). Especially a positive effect was expected on the guild of forest species
81 (Facey et al., 2014) and on the mobile macromoths generally, because these elements enhance
82 the agricultural landscape heterogeneity and provide food sources and shelters for many

species (Benton et al., 2003; Diacon-Bolli et al., 2012; Steiner et al., 2014). On the other hand micromoths tend to be relatively less mobile (Nieminen et al., 1999). Therefore, a stronger response to the grassland management and plant composition was expected compared to the effect of the woody landscape features (Merckx et al., 2009). Although all investigated AES grasslands were extensively managed and could not be cut before 15 June, some were cut later (after 15 July) and in some meadows an uncut grass area was left as a refuge each time it was mown. Accordingly, a positive effect on moth populations of a late mowing regime as well as of decreasing the number of cuts per year was expected (Humbert et al., 2012b; Walter et al., 2007). Presence of uncut refuges was expected to benefit moths too, as it provides continuity of shelter and food resources during the whole season and avoids direct mortality of caterpillars within the refuges (Cizek et al., 2012; Humbert et al., 2010; Kühne et al., 2015; Summerville & Crist, 2004; Šumpich & Konvička, 2012). Due to the Swiss AES regulations, only extensive grazing in fall was authorized on these grasslands, thus low or no effect of grazing was expected (Littlewood, 2008; Pöyry et al., 2005; Stewart & Pullin, 2008).

Given that all meadows included in this study were extensively managed since at least 10 years, and therefore harboured all a relatively diverse vegetation (29 plant species per 16 m^2 on average), the amount of the variation (r^2) explained by the plant species richness was expected to be low for all moth groups (Pöyry et al., 2009; Steiner et al., 2014). Because of their nectar providing properties, the percentage cover of forbs and legumes were expected to have positive effects on moths whereas the percentage cover of grasses was assumed to be neutral.

Materials and Methods

Study sites

For this study, the experimental setup of the grassland project of the Division of Conservation Biology at the University of Bern was used (see Buri et al., 2013). The above mentioned project started in 2010 with the random allocation of different mowing regimes to 47 meadows arranged in twelve areas with four meadows each (except one area with three meadows only) covering the whole Swiss Plateau (Appendix S1). All 47 meadows were registered as extensively managed AES hay meadows since at least 2004 (range 1993–2004), meaning that they could not be fertilized nor cut before 15 June. In about one fourth of all meadows, the first cut was after 15 July and in another fourth, a refuge of 10–20% of the meadow was left when mowing. On average, the meadows were mown twice with a first cut on 29 June (range 15 June – 15 August). There was a minimal distance of 5 km between two areas and a minimal distance of 440 m between two meadows within an area whereas the meadows of one area were all located within a radius of 3.5 km. All meadows had a minimal size of 0.3 ha (range 0.3–1.7 ha).

Moth sampling

In 2014, moths were sampled twice before any meadow were mown (before 15 June) and once after three-fourths of the meadows were mown (between 15 June and 15 July) using light traps, the most common method to sample moths (New, 2004). To reduce the action radius of the light traps, the top half of the surface of the 15 W black light bulbs was masked, resulting in approximately the power of 7.5 W bulbs. The light traps were installed 1.6 m above ground in the middle of each meadow. All meadows of one area were sampled the same night, starting at nightfall and holding for five hours. Moths were euthanized with ethyl acetate and preserved in a freezing box until identification. Macromoths were counted, identified to species level and grouped according to the field guide of Steiner et al. (2014)

130 “Die Nachtfalter Deutschlands” in either openland or forest species. Micromoths were only
131 counted.
132
133 *Environmental variables*
134 The environmental variables were extracted from the Vector 25 data base of the Swiss Federal
135 Office of Topography, using QGIS and SpatiaLite software (Furieri, 2008; Quantum GIS
136 Development Team, 2012) as described in Buri et al. (2014). Percentage of forest, meter of
137 forest edges and meter of hedgerows were quantified within radii of 250 meters around the
138 middle of each meadow. Because the percentage of forest and the meter of forest edges were
139 highly correlated (Spearman correlation coefficient 0.79), the latter was excluded from the
140 analysis. The radius of 250 m was chosen because for moths it has been shown that landscape
141 predictors are most influential within this range (Fuentes-Montemayor et al., 2011) and to
142 limit spatial autocorrelation caused by overlapping radii within areas (Table 1).
143
144 *Management variables*
145 The following information about the management of the meadows from 2010 to 2013 was
146 obtained by questionnaires from the farmers: date of the first cut, number of cuts per year, if
147 an uncut grass refuge was left in the meadow when cut as well as if the meadow was grazed
148 in fall. Regarding the date of the first cut and the number of cuts, the average of the four years
149 was used (Table 1).
150
151 *Vegetation*
152 In spring 2014, before mowing, two vegetation plots of 2 x 4 m separated by 8 m were
153 monitored in each meadow. The purpose of having two plots per meadow was to better
154 capture the small-scale heterogeneity of vegetation patterns. In each plot, all vascular plant
155 species were identified and their respective coverage estimated. Plant species were classified

in three functional groups: grasses (Poaceae, Juncaceae, and Cyperaceae), legumes (Fabaceae) and forbs (other families). The two plots of a meadow were pooled for the species richness analysis and averaged regarding the percentage cover of grass, legume and forb. Because of overlapping plant layers, the summation of the percent covers may exceed 100%.

Statistical analysis

The effects of environment, management and vegetation on moth communities were analysed using generalized linear mixed models (GLMMs). Response variables were the following groups: (a) macromoth openland species abundance, (b) macromoth forest species abundance, (c) macromoth openland species richness, (d) macromoth forest species richness and (e) micromoth abundance. Fixed effects were the environment, management and vegetation variables, random effects were the twelve areas. The models were fitted using either Poisson or Gaussian error distribution and the data was log transformed when necessary. For each of the six response variable groups, the models with best support including only (1) environment, (2) management, or (3) vegetation variables were determined. Models were assessed according to Akaike's information criterion (AIC) using the *dredge* function of the *MuMIn* package (Bartoń, 2015; Johnson & Omland, 2004). Then, the variables remaining in the final environment, management and vegetation models were used for a fourth combined model. Again, out of these variables, the combined model with the lowest AIC was assessed. To extract the marginal as well as the conditional r^2 of all models, the method described by Nakagawa and Schielzeth (2013) was used. The marginal r^2 represents the variance explained by the fixed effects only, and the conditional r^2 describes the variance explained by the fixed plus random effects, i.e. the proportion of variance explained by the model. All analyses were performed using the R version 3.1.0 (R Development Core Team, 2014).

Results

A total of 2'810 macromoths and 1'358 micromoths were collected. The 147 identified macromoth species belonged to the families of *Drepanidae, Erebidae, Lasiocampidae, Limacodidae, Noctuidae, Nolidae, Notodontidae* and *Sphingidae* (Appendix S2). The six most common species represented 52% of all macromoths caught, they were all openland species and belonged to the family of *Noctuidae* (in brackets number of individuals collected): *Agrotis exclamationis* (449), *Charanyca trigrammica* (256), *Hoplodrina blanda* (112), *Mythimna pallens* (126), *Ochropleura plecta* (212) and *Xestia c-nigrum* (318). On average (± standard deviation), 30 (± 35) moths were sampled per meadow and night, 10 (± 19) micromoths and 20 (± 23) macromoths. Regarding macromoths, the average number of species sampled per meadow and night was 8 (± 6). *Smerinthus ocellata,* of which two individuals were caught, one in Cousset and one in Lupfig, was the only national priority species sampled (Bundesamt für Umwelt (ed.), 2011; no red list existing for moths in Switzerland).

Regarding vegetation surveys, in total 155 plant species were recorded with an average of 29 (± 8) species per meadow. On average 66% of the vegetation cover belonged to the most abundant functional group of grasses, 39% to forbs and 13% to legumes.

Environment, management and vegetation models

Table 2 and figure 1 provide a summary of the GLMM models with best support investigating the influence of environment, management, or vegetation on macro- and micromoth communities. Concerning the three groups openland species abundance (Fig. 1a; Table 2a), forest species abundance (Fig. 1b; Table 2b) and forest species richness (Fig. 1d; Table 2d), the environment model, followed by the management model and at last by the vegetation model, had the lowest AIC and the highest r^2 marginal and conditional. For the group openland species richness (Fig. 1c; Table 2c), the management model had the lowest AIC and

207 highest r^2 marginal, but the environment model had the highest r^2 conditional. Regarding
208 micromoth abundance, management and vegetation had the same AIC as well as r^2 marginal,
209 and the r^2 conditional of the vegetation was slightly higher than the value of management.
210 Finally, the environment did not explain any significant part of the variance
211 (Fig. 1e; Table 2e).
212
213 *Retained variables*
214 Compared to the models including only environment, management or vegetation variables,
215 the combined models always showed lowest AIC values (Table 2). All final combined
216 macromoth models retained the fixed effects percentage of forest and meters of hedges (in
217 250 m radius) with significant positive estimates, except for openland species richness where
218 the estimate of forest was not significant. The management variable first cut (Julian day) was
219 found in the openland macromoth species abundance and richness as well as in the forest
220 macromoth species abundance models with a significant negative estimate, whereas the effect
221 was not significant regarding forest species richness. Concerning micromoth abundance, the
222 estimate of first cut was significantly positive. Where refuge (presence of uncut refuge)
223 remained in the final model, it had a negative estimate. This effect was significant in the
224 models of openland species abundance and forest species richness but not for forest species
225 abundance. The variable average number of cuts per year retained in the forest species
226 abundance and openland species richness models had a significant negative estimate. Pasture
227 (occurrence of grazing in autumn) was retained in the final models of forest species
228 abundance and openland species richness with a significant negative estimate. In the group
229 openland species abundance, plant species richness remained in the final model with a
230 negative estimate and in the group forest species abundance, legume coverage was part of the
231 combined model with a positive estimate, but both effects were not significant. In contrast to

this, legume coverage had a significant negative estimate in the final model of micromoth abundance. Regarding r^2, the combined models reached the highest values (Fig. 1).

Discussion

In this study we estimated how much of the variation (in percentage) in the moth assemblages sampled in extensively managed meadows under agri-environment schemes (AES) is explained by surrounding woody landscape features such as hedgerows and forest (250 m radius) and how much by grassland management and plant composition. Results show that a combination of environmental, management and vegetation variables best describes moth abundance and species richness. Depending on the moth group, together these variables explain 10–60% (r^2 marginal) or 47–73% (r^2 conditional) of the variance. The marginal r^2 represents the variance explained by the fixed effects only, and the conditional r^2 describes the variance explained by the fixed plus random effects (Nakagawa & Schielzeth, 2013). In that sense, the r^2 marginal is always $\leq r^2$ conditional and can be considered as a conservative minimum value. Surrounding woody landscape features such as percentage of forest and meters of linear hedges ended up being the most important variables for macromoths. In contrast to this, the less mobile group of micromoths relied more on the grassland management and plant composition of the meadows. In the next subsections, we first present the relative importance of surrounding woody landscape features, grassland management and plant composition, then we discuss the effects and potential mechanisms behind the specific variables retained in the final models of the different moth guilds, and finally we conclude with some management and further research recommendations.

Environment, management and vegetation models

Results show that for forest macromoth abundance and species richness, surrounding woody landscape features are more important predictors than the grassland management and plant

258 composition of the sampled extensively used meadow. For example, 51% (r^2 marginal) of
259 forest species abundance and 46% (r^2 marginal) of forest species richness were explained by
260 the environment, whereas only 15% (r^2 marginal) was explained by the management and even
261 less by the vegetation. The pattern was similar for openland macromoth abundance, but with
262 much lower values; 7% for the environment, 3% for the management and 0% for the
263 vegetation (r^2 marginal). Concerning openland macromoth species richness, the pattern was
264 less clear as the environment (44%) explained more variance than the management (38%)
265 based on r^2 conditional, but based on r^2 marginal the management was with 15% more
266 important than the environment (8%). The overall important influence of the surrounding
267 woody landscape features on macromoth populations found in this study is in accordance with
268 the recent agro-ecological literature on the topic (e.g. Fuentes-Montemayor et al., 2012;
269 Fuentes-Montemayor et al., 2011; Kivinen et al., 2006). Similar patterns have also been
270 shown for butterflies (Flick et al., 2012; Perović et al., 2015; Saarinen et al., 2005), which
271 emphasises that for the conservation of lepidopterans in general, it is necessary to consider the
272 whole landscape matrix (Donald & Evans, 2006; Prevedello & Vieira, 2010; Tscharntke et al.,
273 2005). Nevertheless, our results show that the surrounding woody landscape features are less
274 influential for openland than for forest macromoth species and even uninfluential regarding
275 micromoths. Indeed for micromoths, which can be regarded as low-mobile invertebrates
276 (Nieminen et al., 1999), only local parameters explained some of the observed variances in
277 their abundances (5% by the management and 5% by the vegetation according to r^2 marginal
278 and 63% and 65% respectively according to r^2 conditional). The fact that grassland
279 management also plays a role is not new *per se* and has also been shown previously (Jonason
280 et al., 2013; Pöyry et al., 2005; Šumpich & Konvička, 2012; Taylor & Morecroft, 2009). For
281 example Šumpich and Konvička (2012) demonstrated that management alone (mowing vs
282 abandoning) explained 30% of the variation of macro- and micromoth species compositions
283 sampled in a Czech humid grassland reserve.

Plant composition explained with 0–9% (r^2 marginal; depending on the moth group) the lowest amount of variance in macromoth abundance and species richness. In this study, all sampled meadows were extensively managed for at least the last 10 years (all were registered under Swiss AES with no fertilizer input allowed). Therefore all meadows harboured a relatively high plant diversity and cover of forbs, and thus nectar, compared to conventionally managed meadows (Kleijn et al., 2006). These relatively high plant diversity and low contrast among meadows might be the reason why only a low % of variance in marcomoths was explained by the vegetation. Moth species like *M. pallens* for example appear in non-fertilized habitats only (Steiner et al., 2014), a requirement that was fulfilled by all 47 meadows. Another explanation could be that rather than plant species richness *per se* or coverage of the different plant functional groups, it is the vegetation structure or presence/absence of some host plant species that is important for moths (Axmacher et al., 2009; Kuussaari et al., 2007; Saarinen et al., 2005). In contrast to the macromoths, micromoth abundances were more influenced by the plant composition than the surrounding woody landscape features (see above given values), again emphasizing their relatively stronger dependence on the local conditions (see also Šumpich & Konvička, 2012).

Environmental variables

The environmental variables percentage of forest and meters of hedgerows (within a radius of 250 m of the trapping site) remained in all combined final macromoth models. Effects were significantly positive in all but the openland species richness model, where the effect of forest was not significant. This means that such structures are important not only for forest macromoths but also for openland macromoths, at least for their abundances. These effects were expected, not only forests are known to provide habitat for many moth species, it has been shown that forest fragments in agricultural landscapes are surrounded by high species richness and abundance of moths (Ricketts et al., 2001). Merckx et al., (2010; 2012) showed

310 that the presence of hedgerow trees locally increased species richness of macromoths and that
311 the effect was particularly strong for shrub and tree feeding moth species. 14% of the
312 macromoths sampled in our study were forest species, which feed on shrub and trees, in
313 addition, the majority of the sampled openland macromoth species are generalists and their
314 caterpillars can feed on shrubs and herbaceous plants. To this, hedgerows provide shelter and
315 permanent horizontal structures and thereby enhance spatial heterogeneity which has been
316 shown to be a key factor for biodiversity in general (Diacon-Bolli et al., 2012;
317 Perović et al., 2015). Furthermore, like forest edges, hedgerows harbour plenty of herbaceous
318 plants that may act as nectar source for adult moths and/or feeding plants for their caterpillars
319 (Steiner et al., 2014).
320
321 *Management variables*
322 Postponing the first mowing date from mid-June to mid-July was expected to be positive for
323 all macromoths, because it generally allows more invertebrates to achieve their reproduction
324 cycle before any mowing event (Humbert et al., 2012b; Valtonen et al., 2006; Walter et al.,
325 2007). In our study, this hypothesis was confirmed for micromoths; they benefited from a
326 mid-summer cut. On the other hand, the negative effects of delaying the first cut observed on
327 openland species abundance and richness as well as on forest species abundance came as a
328 surprise. These negative effects can be either because a cut in mid of June is beneficial or
329 because mowing mid of July is detrimental. All of the most numerous macromoth species of
330 our study (i.e. *A. exclamationis*, *C. trigrammica*, *H. blanda*, *M. pallens*, *O. plecta* and *X. c-*
331 *nigrum*) are still flying in July. Consequently, a cut in mid of July encounter species with a
332 late phenology, for example *H. blanda,* or a species with two generations like *M. pallens* in
333 their sensitive life-stage (i.e. caterpillar or pupae). Postponing mowing to late-summer
334 (August or September) might therefore be required to favour these macromoth species
335 (Valtonen et al., 2006). In contrast to a mid-summer cut, an earlier but patchy mowing regime

336 is promising because it leaves uncut areas throughout the whole season (Cizek et al., 2012;
337 Humbert et al., 2012a; Šumpich & Konvička, 2012). However, our results show that leaving a
338 refuge did not fulfil these expectations. Regarding openland species abundance and forest
339 species richness, an unmown refuge of 10–20% of the meadow even negatively affected
340 them. While we are not aware of any other study that investigated the effect of leaving a
341 refuge on moths, the negative response found here contrasts to the usual reported positive
342 effects of leaving an uncut grass refuge on butterflies (Konvicka et al., 2008; Kühne et al.,
343 2015), orthopterans (Buri et al., 2013; Humbert et al., 2012a), and many other field
344 invertebrate groups (e. g. Buri et al., 2014; Cizek et al., 2012). One explanation for this
345 phenomenon could be methodological; because of its attractiveness for moths, the refuge
346 competes with the light trap, resulting in lower sampling success. The variable number of cuts
347 per year remained in the final models of forest species abundance and openland species
348 richness with a significant negative estimate. This is in accordance with our expectations as
349 the direct negative effect of the meadow harvesting process on invertebrates had been shown
350 by several studies (Dover et al., 2010; Helden & Leather, 2004; Humbert et al., 2010;
351 Humbert et al., 2009). Pasture, the fourth management variable, was found with a significant
352 negative estimate in the final model of forest species abundance and openland species
353 richness. This negative impact of grazing on lepidopterans had also been shown by scientists
354 before (Fuentes-Montemayor et al., 2012; Kruess & Tscharntke, 2002; Littlewood, 2008;
355 Pöyry et al., 2005), especially caterpillars (van Noordwijk et al., 2012).
356
357 *Vegetation variables*
358 The only vegetation variable that was retained in one of the models was % cover of legume.
359 While its effect was not significant for forest macromoth abundance, it had, in contrast to our
360 expectation, a significant negative effect on micromoth abundance. This does not necessarily
361 mean that legumes are harmful for micromoths, as the negative effect could be due to an

362 indirect effect such as competition between legumes and other 'beneficial' plants, but at least
363 it shows that micromoths do not rely on legumes as principal host plants or nectar source.
364 Almost all of the sampled macromoth species do not have strong preferences towards a
365 particular food plant and are therefore considered generalists, which may explain the missing
366 effect of plant species richness and % cover of the plant functional groups on any investigated
367 macromoth guild in this study. We argue that the presence of a particular plant species or
368 family or the indirect effects of plant diversity, such as the provided structure
369 (Andrey et al., 2014), may be more important and crucial vegetation features for moths than
370 plant species richness *per se* (Axmacher et al., 2009; Berg et al., 2013; Jonason et al., 2013;
371 Saarinen et al., 2005).
372
373 **Conclusion and management recommendations**
374 Altogether, results demonstrate the importance of the presence of woody elements in
375 agricultural landscapes in addition to the common AES field-scale management measures
376 applied for the conservation of the entire moth community. Specifically, to support the adult
377 life stage of macromoths, we recommend the implementation of a mosaic of semi-natural
378 woody structures such as hedges, and if possible forest patches, and extensively managed
379 meadows at a 250 m radius scale. Regarding micromoths we also recommend a mid-summer
380 (15 July or later) first possible cut, although this mowing regime may have a negative effect
381 on the macromoths, which emphasizes that there is no single appropriate mowing time that
382 suits all organisms (Birkhofer et al., 2015; Cizek et al., 2012; Humbert et al., 2012b).
383 Among the most numerous moth species (all openland species) found in our study, habitat
384 and food requirements of caterpillars are very diverse and vary from living in the soil and
385 feeding on roots (*A. exclamationis*) to living close to the ground (*C. trigrammica*), feeding on
386 grasses (*M. pallens*) or being a generalist and feeding on various forb and shrub plants or
387 hedges (*H. blanda, O. plecta and X. c-nigrum*). Therefore, to draw more specific management

recommendations, we strongly advocate further research on the topic that include and investigate the requirements of the caterpillars (Öckinger, 2008).

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Table 1. Environment, management and vegetation variables included in the linear regression analyses.

Environment		
Forest	[%]	250 m radius
Forest edges	[m]	250 m radius
Hedgerows	[m]	250 m radius
Elevation	[m]	Altitude
Management		
First cut	Julian day	Average from 2010–2013
Number of cuts		Per year, average from 2010–2013
Grazing	Yes/No	
Refuge	Yes/No	
Vegetation		
Plant species richness		Number of species
Grasses	[%]	Cover
Legumes	[%]	Cover
Forbs	[%]	Cover

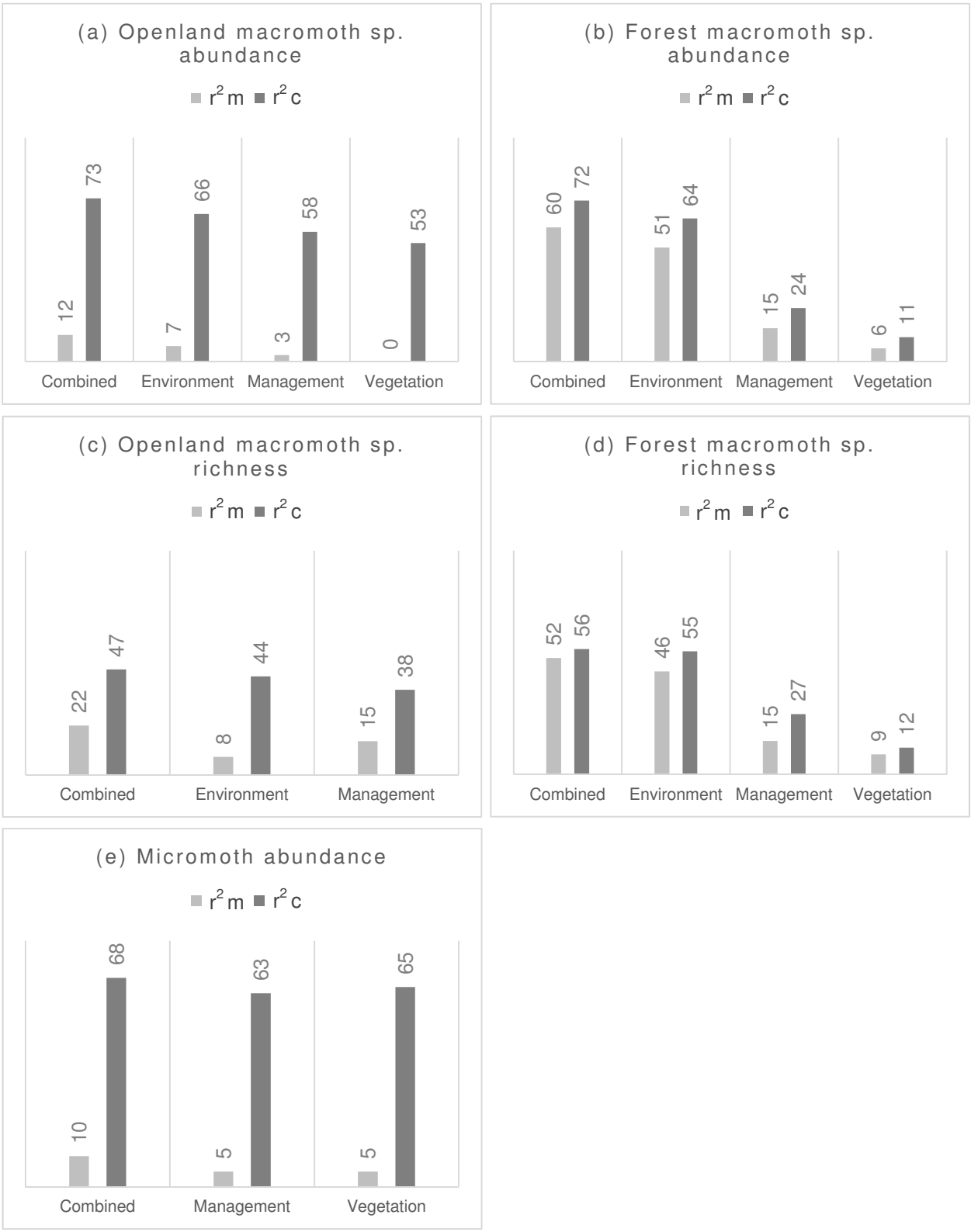
Table 2. Summary of the GLMM outputs of the final models investigating the influence of environment, management, vegetation and a combination of such variables on: (a) openland macromoth species abundance, (b) forest macromoth species abundance, (c) openland macromoth species richness, (d) forest macromoth species richness and (e) micromoth abundance. The variables remaining in the final models of environment, management and vegetation were used to determine the best combined models. Models were assessed using Akaike's information criterion (AIC). The mean and standard deviation (SD) number of moths sampled per meadow are provided.

		Environment				Management				Vegetation				Combined			
(a)	**Openland macromoth sp. abundance**	AIC: 573				AIC: 610				AIC: 639				AIC: 516			
	Mean: 50; SD: 38	*Fixed effects*	*Estimate*	*SE*	*P*	*Fixed effects*	*Estimate*	*SE*	*P*	*Fixed effects*	*Estimate*	*SE*	*P*	*Fixed effects*	*Estimate*	*SE*	*P*
		Forest [%]	0.6380	0.13	**< 0.001**	1st cut (day)	-0.0067	< 0.01	**< 0.001**	Sp. Richness	-0.0107	< 0.01	**0.006**	Forest [%]	0.3218	0.16	**0.043**
		Hedges [m]	0.0015	< 0.01	**< 0.001**	Refuge (yes)	-0.3052	0.05	**< 0.001**					Hedges [m]	0.0018	< 0.01	**< 0.001**
														1st cut (day)	-0.0067	< 0.01	**< 0.001**
														Refuge (yes)	-0.4146	0.07	**< 0.001**
														Sp. Richness	-0.0078	< 0.01	0.099
(b)	**Forest macromoth sp. abundance**	AIC: 290				AIC: 357				AIC: 402				AIC: 276			
	Mean: 8; SD: 8	*Fixed effects*	*Estimate*	*SE*	*P*	*Fixed effects*	*Estimate*	*SE*	*P*	*Fixed effects*	*Estimate*	*SE*	*P*	*Fixed effects*	*Estimate*	*SE*	*P*
		Forest [%]	3.5734	0.34	**< 0.001**	1st cut (day)	-0.0260	< 0.01	**< 0.001**	Sp. Richness	0.0231	0.01	**0.010**	Forest [%]	3.1242	0.37	**< 0.001**
		Hedges [m]	0.0021	< 0.01	**< 0.001**	Nb cuts	-0.5678	0.19	**0.003**	Grass [%]	-0.0044	< 0.01	0.100	Hedges [m]	0.0025	< 0.01	**< 0.001**
						Refuge (yes)	-0.5000	0.15	**0.001**	Legume [%]	-0.0188	0.01	**0.001**	1st cut (day)	-0.0193	0.01	**< 0.001**
						Pasture (yes)	-0.6945	0.16	**< 0.001**					Nb cuts	-0.6964	0.20	**< 0.001**
														Refuge (yes)	-0.2708	0.18	0.128
														Pasture (yes)	-0.4159	0.15	**0.007**
														Legume [%]	0.0131	0.01	0.052
(c)	**Openland macromoth sp. richness**	AIC: 293				AIC: 291				AIC: 293				AIC: 288			
	Mean: 15; SD: 5	*Fixed effects*	*Estimate*	*SE*	*P*	*Fixed effects*	*Estimate*	*SE*	*P*	*Fixed effects*	*Estimate*	*SE*	*P*	*Fixed effects*	*Estimate*	*SE*	*P*
		Forest [%]	5.7805	3.70	**0.125**	1st cut (day)	-0.1002	0.05	0.071	0-model				Forest [%]	5.7638	3.37	0.094
		Hedges [m]	0.0090	< 0.01	0.061	Nb cuts	-5.3024	2.06	**0.013**					Hedges [m]	0.0109	< 0.01	**0.016**
						Pasture (yes)	-3.2184	1.49	**0.035**					1st cut (day)	-0.1019	0.05	**0.046**
														Nb cuts	-6.3023	1.95	**0.002**
														Pasture (yes)	-2.8541	1.40	**0.046**
(d)	**Forest macromoth sp. richness**	AIC: 236				AIC: 267				AIC: 277				AIC: 234			
	Mean: 6; SD: 4	*Fixed effects*	*Estimate*	*SE*	*P*	*Fixed effects*	*Estimate*	*SE*	*P*	*Fixed effects*	*Estimate*	*SE*	*P*	*Fixed effects*	*Estimate*	*SE*	*P*
		Forest [%]	2.4105	0.39	**< 0.001**	1st cut (day)	-0.0132	0.01	**0.009**	Sp. Richness	0.0252	0.01	**0.009**	Forest [%]	2.0133	0.39	**< 0.001**
		Hedges [m]	0.0020	< 0.01	**< 0.001**	Refuge (yes)	-0.4408	0.17	**0.009**					Hedges [m]	0.0020	< 0.01	**< 0.001**
						Pasture (yes)	-0.3762	0.16	**0.018**					1st cut (day)	-0.0085	0.01	0.093
														Refuge (yes)	-0.4207	0.18	**0.022**
(e)	**Micromoth abundance**	AIC: 132				AIC: 129				AIC: 129				AIC: 125			
	Mean: 29; SD: 45	*Fixed effects*	*Estimate*	*SE*	*P*	*Fixed effects*	*Estimate*	*SE*	*P*	*Fixed effects*	*Estimate*	*SE*	*P*	*Fixed effects*	*Estimate*	*SE*	*P*
		null model				1st cut (day)	0.0175	0.01	**0.021**	Legume [%]	-0.0222	0.01	**0.027**	1st cut (day)	0.0168	0.01	**0.019**
														Legume [%]	-0.0214	0.01	**0.025**

Figure Legend

Figure 1. Percentages of variance explained by the environment, management, vegetation and combined models (combination of environment, management and vegetation variables) for: (a) openland macromoth species abundance, (b) forest macromoth species abundance, (c) openland macromoth species richness, (d) forest macromoth species richness and (e) micromoth abundance. Marginal r^2 (r^2 m, light-grey) represents the percentage explained by the fixed effects only whereas conditional r^2 (r^2 c, dark-grey) is the percentage explained by both fixed plus random effects. Vegetation is absent in openland species richness, and environment is absent in micromoth abundance, because respective models with best support were the null-models (see Table 2).

Figure 1.


(a) Openland macromoth sp. abundance
r2 m r2 c
12
73
7
66
3
58
0
53
Combined
Environment
Management
Vegetation
(b) Forest macromoth sp. abundance
r2 m r2 c
60
72
51
64
15
24
6
11
Combined
Environment
Management
Vegetation
(c) Openland macromoth sp. richness
r2 m r2 c
22
47
8
44
15
38
Combined
Environment
Management
(d) Forest macromoth sp. richness
r2 m r2 c
52
56
46
55
15
27
9
12
Combined
Environment
Management
Vegetation
(e) Micromoth abundance
r2 m r2 c
10
68
5
63
5
65
Combined
Management
Vegetation

Appendix S1. Geographic coordinates of all meadows with the total number of moth individuals and species sampled per meadow.

area	canton	GPS coordinates E [CH1903]	GPS coordinates N [CH1903]	total abundance	macromoth abundance	micromoth abundance	openland sp. abundance	forest sp. abundance	openland sp. richness	forest sp. richness
Avenches	VD	567193	197127	65	45	20	32	12	17	1
Avenches	VD	566771	196996	84	75	9	62	13	26	11
Avenches	VD	570876	198726	68	45	23	37	6	15	4
Avenches	VD	571156	199189	50	27	23	22	5	13	5
Belp	BE	605487	192366	200	187	13	146	38	27	12
Belp	BE	605869	193107	140	131	9	122	6	18	4
Belp	BE	602699	195929	141	115	26	109	5	20	4
Belp	BE	605992	193887	83	67	16	64	2	17	1
Coffrane	NE	556126	205774	62	52	10	44	4	20	4
Coffrane	NE	555499	206934	58	52	6	41	6	18	6
Coffrane	NE	555200	206511	36	29	7	21	6	11	5
Cousset	FR	565063	185881	79	63	16	42	19	20	13
Cousset	FR	564697	185486	63	48	15	36	11	17	9
Cousset	FR	564488	185974	129	79	50	68	8	17	8
Cousset	FR	566709	186749	36	27	9	23	4	11	3
Diegten	BL	628587	252768	419	155	264	142	9	19	9
Diegten	BL	628895	252035	257	116	141	98	15	17	10
Diegten	BL	629724	254270	191	110	81	92	15	20	8
Diegten	BL	628554	251603	232	174	58	161	8	26	8
Grossaffoltern	BE	595281	212666	33	27	6	21	5	8	5
Grossaffoltern	BE	592103	214070	50	42	8	20	20	12	14
Grossaffoltern	BE	595164	213838	37	26	11	15	11	9	8
Grossaffoltern	BE	593100	212533	39	30	9	28	2	10	2
Hindelbank	BE	612352	209751	52	46	6	36	9	10	5
Hindelbank	BE	608282	208143	32	30	2	17	13	10	7
Hindelbank	BE	608715	211818	46	35	11	21	11	13	8
Hindelbank	BE	609796	208848	44	41	3	31	10	15	7
Huttwil	BE	628558	215769	43	33	10	33	0	12	0
Huttwil	BE	630859	216684	100	61	39	57	4	15	4
Huttwil	BE	631454	217636	181	65	116	60	3	13	3
Huttwil	BE	629144	217791	59	38	21	28	10	10	5
Lupfig	AG	655871	255464	145	90	55	88	2	14	2
Lupfig	AG	656968	254806	161	123	38	104	16	22	11
Lupfig	AG	656488	254973	92	54	38	51	2	14	2
Lupfig	AG	658689	255134	115	47	68	45	0	13	0
Nyon	VD	506251	141110	42	36	6	32	4	14	3
Nyon	VD	503625	137146	60	40	20	39	1	10	1
Nyon	VD	504394	137098	43	31	12	28	3	13	2
Nyon	VD	508935	140280	46	26	20	25	0	12	0
Orbe	VD	528474	173673	37	29	8	27	1	13	1
Orbe	VD	526781	172298	121	106	15	72	31	27	15
Orbe	VD	527588	172614	33	16	17	13	2	11	2
Orbe	VD	528116	174457	15	15	0	10	5	6	4
Wohlen	BE	595389	205416	17	8	9	2	6	2	5
Wohlen	BE	598193	203540	48	47	1	38	9	15	9
Wohlen	BE	598952	205162	20	14	6	12	2	7	2
Wohlen	BE	596265	202101	64	57	7	46	10	13	9

Appendix S2. List of the macromoth species identified and their respective main habitat (forest vs openland). *Noctuidae sp.* and *Geometridae sp.* contain all unidentified individuals of that family.

species	family	main habitat	individuals
Dendrolimus pini	*Lasiocampidae*	forest	9
Macrothylacia rubi	*Lasiocampidae*	openland	1
Malacosoma neustria	*Lasiocampidae*	forest	17
Agrius convolvuli	*Sphingidae*	openland	2
Deilephila elpenor	*Sphingidae*	openland	1
Deilephila porcellus	*Sphingidae*	openland	3
Laothoe populi	*Sphingidae*	forest	4
Mimas tiliae	*Sphingidae*	forest	1
Smerinthus ocellata	*Sphingidae*	forest	2
Sphinx ligustri	*Sphingidae*	forest	2
Habrosyne pyritoides	*Drepanidae*	forest	13
Tethea or	*Drepanidae*	forest	3
Thyatira batis	*Drepanidae*	forest	2
Watsonalla cultraria	*Drepanidae*	forest	7
Clostera curtula	*Notodontidae*	forest	1
Clostera pigra	*Notodontidae*	forest	2
Drymonia dodonaea	*Notodontidae*	forest	11
Drymonia ruficornis	*Notodontidae*	forest	1
Harpyia milhauseri	*Notodontidae*	forest	1
Notodonta dromedarius	*Notodontidae*	forest	4
Notodonta ziczac	*Notodontidae*	forest	1
Peridea anceps	*Notodontidae*	forest	8
Phalera bucephala	*Notodontidae*	forest	31
Pterostoma palpina	*Notodontidae*	forest	5
Ptilodon capucina	*Notodontidae*	forest	2
Stauropus fagi	*Notodontidae*	forest	2
Abrostola tripartita	*Noctuidae*	openland	1
Aedia funesta	*Noctuidae*	openland	1
Agrotis cinerea	*Noctuidae*	openland	2
Agrotis clavis	*Noctuidae*	openland	17
Agrotis exclamationis	*Noctuidae*	openland	449
Agrotis segetum	*Noctuidae*	openland	6
Anaplectoides prasina	*Noctuidae*	forest	5
Apamea anceps	*Noctuidae*	openland	2
Apamea crenata	*Noctuidae*	openland	1
Apamea monoglypha	*Noctuidae*	openland	22
Apamea scolopacina	*Noctuidae*	forest	1
Apamea sordens	*Noctuidae*	openland	10
Apamea sp	*Noctuidae*	openland	1
Apamea sublustris	*Noctuidae*	openland	2
Arylia putris	*Noctuidae*	openland	19
Autographa gamma	*Noctuidae*	openland	11
Cerastis rubricosa	*Noctuidae*	openland	1
Charanyca trigrammica	*Noctuidae*	openland	256
Colocasia coryli	*Noctuidae*	forest	38
Conistra rubiginea	*Noctuidae*	openland	1
Cosmia trapezina	*Noctuidae*	forest	2
Craniophora ligustri	*Noctuidae*	forest	1
Cucullia umbratica	*Noctuidae*	openland	1

Diachrysia chrysitis	*Noctuidae*	openland	6
Diachrysia stenochrysis	*Noctuidae*	openland	7
Diarsia brunnea	*Noctuidae*	openland	5
Egira conspicillaris	*Noctuidae*	openland	1
Euchalcia variabilis	*Noctuidae*	forest	1
Euplexia lucipara	*Noctuidae*	forest	3
Hada plebeja	*Noctuidae*	openland	3
Hoplodrina ambigua	*Noctuidae*	openland	16
Hoplodrina blanda	*Noctuidae*	openland	112
Hoplodrina octogenaria	*Noctuidae*	openland	83
Hoplodrina respersa	*Noctuidae*	openland	3
Ipimorpha subtusa	*Noctuidae*	forest	1
Lacanobia w-latinum	*Noctuidae*	openland	13
Lacanobia oleracea	*Noctuidae*	openland	22
Lacanobia sp	*Noctuidae*	openland	1
Lacanobia suasa	*Noctuidae*	openland	10
Lacanobia thalassina	*Noctuidae*	openland	2
Mamestra brassicae	*Noctuidae*	openland	2
Melanchra persicariae	*Noctuidae*	openland	1
Mesapamea secalis	*Noctuidae*	openland	1
Mesapamea sp	*Noctuidae*	openland	17
Mesoligia furuncula	*Noctuidae*	openland	1
Mythimna albipuncta	*Noctuidae*	openland	60
Mythimna conigera	*Noctuidae*	openland	4
Mythimna impura	*Noctuidae*	openland	17
Mythimna pallens	*Noctuidae*	openland	126
Mythimna vitellina	*Noctuidae*	openland	1
Noctua comes	*Noctuidae*	openland	6
Noctua fimbriata	*Noctuidae*	openland	2
Noctua janthe	*Noctuidae*	openland	1
Noctua pronuba	*Noctuidae*	openland	22
Ochropleura plecta	*Noctuidae*	openland	212
Oligia strigilis	*Noctuidae*	openland	42
Orthosia cerasi	*Noctuidae*	openland	1
Orthosia gothica	*Noctuidae*	openland	8
Pachetra sagittigera	*Noctuidae*	openland	1
Panolis flammea	*Noctuidae*	forest	1
Phlogophora meticulosa	*Noctuidae*	openland	2
Polia nebulosa	*Noctuidae*	openland	3
Pyrrhia umbra	*Noctuidae*	openland	3
Rusina ferruginea	*Noctuidae*	forest	11
Sideridis reticulata	*Noctuidae*	openland	1
Subacronicta megacephala	*Noctuidae*	forest	3
Trachea atriplicis	*Noctuidae*	openland	2
Tyta luctuosa	*Noctuidae*	openland	1
Xestia c-nigrum	*Noctuidae*	openland	318
Xestia ditrapezium	*Noctuidae*	openland	2
Xestia triangulum	*Noctuidae*	openland	7
Noctuidae sp	*Noctuidae*		18
Pseudopis prasinana	*Nolidae*	forest	40
Arctornis l-nigrum	*Erebidae*	forest	1
Atolmis rubricollis	*Erebidae*	forest	18
Calliteara pudibunda	*Erebidae*	openland	64
Diacrisia sannio	*Erebidae*	openland	49
Diaphora mendica	*Erebidae*	openland	27
Eilema complana	*Erebidae*	openland	2

Eilema griseola	*Erebidae*	forest	1
Eilema lurideola	*Erebidae*	openland	33
Eilema sororcula	*Erebidae*	forest	12
Euclidia glyphica	*Erebidae*	openland	3
Euproctis chrysorrhoea	*Erebidae*	openland	4
Lasperyria flexula	*Erebidae*	forest	1
Lithosia quadra	*Erebidae*	forest	1
Miltochrista miniata	*Erebidae*	openland	22
Phragmatobia fuliginosa	*Erebidae*	openland	3
Spilarctia lutea	*Erebidae*	openland	41
Spilosoma lubricipeda	*Erebidae*	openland	60
Apoda limacodes	*Limacodidae*	forest	4
Alcis repandata	*Geometridae*	forest	22
Angerona prunaria	*Geometridae*	forest	6
Biston betularia	*Geometridae*	forest	13
Bupalus piniaria	*Geometridae*	forest	4
Chiasmia clathrata	*Geometridae*	openland	53
Chloroclysta siterata	*Geometridae*	openland	2
Colostygia aptata	*Geometridae*	openland	3
Cyclophora linearia	*Geometridae*	forest	4
Ectropis crepuscularia	*Geometridae*	openland	1
Epirrhoe rivata	*Geometridae*	openland	4
Hypomecis roboraria	*Geometridae*	forest	3
Hypometics punctinalis	*Geometridae*	forest	4
Idaea aversata	*Geometridae*	openland	2
Idaea deversaria	*Geometridae*	openland	1
Idaea sp	*Geometridae*	openland	1
Lampropteryx suffumata	*Geometridae*	forest	3
Ligdia adustata	*Geometridae*	forest	4
Lomaspilis marginata	*Geometridae*	forest	7
Lomographa temerata	*Geometridae*	forest	1
Lycia hirtaria	*Geometridae*	forest	2
Macaria alternata	*Geometridae*	forest	2
Macaria wauaria	*Geometridae*	forest	9
Ochropacha duplaris	*Geometridae*	forest	1
Odontopera bidentata	*Geometridae*	forest	11
Opisthograptis luteolata	*Geometridae*	openland	6
Peribatodes rhomboidaria	*Geometridae*	openland	7
Perozima alchemillata	*Geometridae*	openland	2
Petrophora chlorosata	*Geometridae*	forest	4
Scopula immorata	*Geometridae*	openland	8
Selenia dentaria	*Geometridae*	forest	2
Selenia lunularia	*Geometridae*	forest	7
Siona lineata	*Geometridae*	openland	3
Thera variata	*Geometridae*	forest	1
Xanthorhoe quadrifasiata	*Geometridae*	openland	1
Xanthorhoe spadicearia ferrugata	*Geometridae*	openland	1
Geometridae sp	*Geometridae*		47
total abundance			**4168**
macrolepidoptera abundance			**2810**
macrolepidoptera sp. richness			**147**
openland abundance			**2361**
openland species richness			**86**
forest abundance			**384**
forest species richness			**61**