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Moths and management of a grassland reserve: regular mowing and temporary abandonment support different species

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Abstract: Although reserves of temperate seminatural grassland require management interventions to prevent succesional change, each intervention affects the populations of sensitive organisms, including insects. Therefore, it appears as a wise bet-hedging strategy to manage reserves in diverse and patchy manners. Using portable light traps, we surveyed the effects of two contrasting management options, mowing and temporary abandonment, applied in a humid grassland reserve in a submountain area of the Czech Republic. Besides of Macrolepidoptera, we also surveyed Microlepidoptera, small moths rarely considered in community studies. Numbers of individiuals and species were similar in the two treatments, but ordionation analyses showed that catches originating from these two treatments differed in species composition, management alone explaining ca 30 per cent of variation both for all moths and if split to Marcolepidoptera and Microlepidoptera. Whereas a majority of macrolepidopteran humid grassland specialists preferred unmown sections or displayed no association with management, microlepidopteran humid grassland specialists contained equal representation of species inclining towards mown and unmown sections. We thus revealed that even mown section may host valuable species; an observation which would not have been detected had we considered Macrolepidoptera only. Our results highlight the necessity of diversified management, including temporary abandonment, to conserve the biodiversity of grassland reserves and grasslands in general.

Key words: Lepidoptera; heterogeneity; seminatural meadow; reserve management; temperate grassland

Introduction

A considerable part of European biodiversity depends on grasslands historically maintained by activities such as hay making or grazing, practised in a traditional nonintensive manner (Duffey et al. 1974; Sammul et al. 2008; Dover et al. 2011). Reserves protecting seminatural grasslands require management simulating traditional farming practices. If left unmanaged, succession first causes plant diversity declines due to dominance of a few competitively superior plants, and ultimately scrub and forest encroachement (Petříček & Míchal 1999; Middleton et al. 2006; Billeter et al. 2007).

The grassland conservation management must be executed with care. Whereas a majority of plants growing at seminatural grassland will, by default, regenerate after hay cutting or grazing (e.g., Hegland et al. 2001; Bissels et al. 2004; but see Kohler et al. 2005), populations of specialised and relatively sedentary animals, including insects, may be negatively affected. Export of biomass depletes insect of food and shelter (Morris 2000; Kruess & Tscharntke 2002; Huntzinger et al. 2008) and directly kills individuals (Schtickzelle et al. 2007; Dover et al. 2010; Humbert et al. 2010). A serious risk concerns vegetation homogenisation, caused by applying identical management techniques over large areas. Many insects require diverse resources situated within short dispersal distances (Dennis et al. 2003; Ouin et al. 2004). While former small-scale farming maintained rich and finely-scaled habitat mosaics (Spitzer et al. 2009; Dover et al. 2011), insular reserves often represent the last refuges for sensitive species in intensively farmed landscapes (Samways 2005; Ekroos et et. 2010).

The effects of various methods of grassland management on invertebrates are currently intensively studied throughout Europe in connection with the EU agricultural policy reform, which aims to reward farmers for biologically more benign farming (Critchley et al. 2004; Kuussaari et al. 2007; Brereton et al. 2008). Some studies targeted entire landscapes, comparing management impacts on insects over large scales (Bergman et al. 2004; Wickramasinghe et al. 2004). They typically relied on a few model groups, such as butterflies (Öckinger & Smith 2006; Rundlöf et al. 2008), or bumblebees (Haaland & Gyllin 2010), although multi-taxa comparisons also exist (Meek et al. 2002; Roth et al. 2008; Sjodin et al. 2008; Čížek et al. 2012).

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Here we take a different approach, studying the local-scale response of a diverse group of insect herbivores, namely nocturnal moths (Lepidoptera). We assess the moths' response to two contrasting regimes, mowing and abandonment, within a middle-sized fenland reserve. Unlike studies restricted to Macrolepidoptera, or macro-moths (e.g., Woiwod & Hanski 1992; Grand & Mello 2004; Littlewood 2008; Mutshinda et al. 2008; Merckx et al. 2009a, b), we also included Microlepidoptera (micro-moths), which are more difficult for handling and identification and hence rarely considered in ecology studies (but see Fuentes-Montemayor et al. 2011; Summerville et al. 2001). We expected that due to small body sizes, Microlepidoptera might contain a higher number of specialised sedentary species, and should be more sensitive to impacts of site management (e.g., Vávra et al. 1996; Spitzer et al. 1999; Šumpich 2006; Summerville et al. 2007).

Specifically, we asked how the two different management regimes affect the species composition, paying particular emphasis on a group of humid grassland specialists. We also compare Microlepidoptera and Macrolepidoptera in order to assess relative utility of these two groups for studying effects of habitat management on insect communities.

Material and methods

Study system and moth sampling

Kamenná Touba reserve (49°36′ N, 15°24′ E, alt. 465 m a.s.l., area 45 ha) protects a highland fen at the spring area of Pstruží brook, Ceskomoravská Highlands, Czech Republic. A flat-surfaced depression, coveded by wet cirsium meadows (*Angelico-Cirsietum palustris*) and acidic moss-rich fens (*Caricion fuscae*) (cf. Chytrý et al. 2001), is surrounded by improved grasslands, arable land and spruce plantations. Traditional management was hay harvest for leaf litter or low-quality fodder, varying in intensity among years. This terminated in the 1980s, while farming intensification in the wide environment isolated the site from other similar habitats. Following establishment of the reserve in 1993, mowing once a year was reestablished for a half of the reserve area, whereas the other half remains unmanaged.

The moths were sampled using portable light traps, consisting of an actinic fluorescent tube (8 W/12 V) with prevailing UV radiance attached to a 10 L plastic container with a chlorophorme-filled vial. The energy source was a rechargeable battery (7 Ah/12 V) with photoelectric switch.

Six traps operated from June to August, 2003, covering the flight period of a majority of moth species in this submountain region (Dvořák & Šumpich 2005). They were set at fixed sites, three at the mown and three at the unmown sextion, with the minimum trap-to-trap distances being 200 m, and the minimum distances to the edges or mown/unmown sections bein 100 m. Because the vegetation height varied during the year and among sections, the traps were, if necessary, installed onto socles so that the fluorescent tubes overtopped the sward. They were set for one-night intervals approximately fortnightly, in June 4, 12, 29; July 20, 26; August 5, 9, 18 and 29. All moths captured were identified to species level, using genital preparations if necessary.

Moth groupings and delimitation of specialists

Moth system and nomenclature follow Lastuvka (1998). The two groups distinguished here, Macrolepidoptera and Microlepidoptera, are non-phylogenetic groupings of families containing predominately large-bodied and small-bodied species, respectively. We delimit them in a traditional way (e.g., Sterneck 1929) so that Macrolepidoptera include the evolutionarily derived Macrolepidoptera clade (*sensu* Kristensen et al. 2008), plus the more primitive Hepialidae, Zygaenidae and Limacodidae. All remaining families compose Microlepidoptera.

The delimitation of humid grassland specialists (herein: specialists) follows Šumpich et al. (2003), who assessed the habitat requirements of all Czech Republic Lepidoptera, assigning individual species to habitat types recognised by Chytrý et al. (2001).

Statistical analysis

Principal component analysis (PCA), an indirect multivariate method extracting gradients in the species composition of samples, was used to visualise the species composition of catches. We computed it in CANOCO, v. 4.1 (Ter Braak & Smilauer 1998), on square-root transformed species data, using the following options: downweighting of rare species, scalling focused on inter-species correlations, species scores divided by standard deviations.

Whereas indirect ordination methods such as PCA reveal main gradients in community data, direct methods relate such gradients to external predictors and test the importance of these predictors using permutation-based significance tests. We used one such method, the canonical correspondence analysis (CCA), followed by the the Monte-Carlo permutation test, computed with the following CANOCO options: square-root transformation of species counts, downweighting of rare species, scaling focused on inter-species distances. We computed two versions of the analysis, one for data summed across all trapping nights, allowing a comparison of explained variation with the indirect PCA analysis, and one reflecting the temporal aspect of the sampling. For the latter, we used a split-plot permutation design, permuting the subsequent trapping visits using cyclic shifts, while the six traps (whole plots) were permuted in random.

Results

The grand total of all catches was 372 species/5022 individuals (Microlepidoptera: 157/2014, Macrolepidoptera: 215/3008). Total means/medians per trap were, for species, 169.7 (± 27.8 SD)/173, and for individuals, 837 (± 189.8 SD)/863. The respective numbers for Microlepidoptera were 68.2 (± 11.4 SD)/73 species and 335.7 (± 111.7 SD)/340 individuals, and for Macrolepidoptera 101.2 (±24.3 SD)/102.5 species and 501.3 (± 47.8 SD)/526 individuals. Humid grassland specialists were represented by 41 species/895 individuals, 21/385 representing Microlepidoptera and 20/510 representing Macrolepidoptera. The low number of replicates precluded comparing the catches from mown and unmown sections using a formal test, but the means and standard deviations (Table 1) suggest that the numbers were very similar quantitatively.

PCA ordinations (Table 2) separated mown and unmown sections along the first ordination axis, explaining a third of variation in species data. When

Table 1. Mean numbers of species and individuals of moths trapped into portable light traps set to mown and umnown sections of the Kamenna trouba reserve, plus accompanying standard deviations. There were three traps per treatment, each operating for nine nights, the numbers are based on sums from all trapping nights. "Specialists" are species restricted to varius humid grassland and fenland habitats (see text for details).

	Mean mown	±SD	Mean unmown	±SD
Microlepidoptera species	65	15.9	72	7.5
Microlepidoptera individuals	293	131.8	378	92.2
Macrolepidoptera species	117	13.1	85	22.3
Macrolepidoptera individuals	592	75.2	411	156.5
Total species	183	23.3	156	29.3
Total individuals	888	162.9	789	238.0
Specialist Microlepidoptera species	11	2.5	12	0.0
Specialist Microlepidoptera individuals	67	41.3	61	4.4
Specialist Macrolepidoptera species	16	1.5	15	3.0
Specialist Macrolepidoptera individuals	63	14.6	107	57.1
All specialist species	27	3.5	27	3.0
All specialist individuals	130	53.4	168	59.8

Table 2. Results of ordination analyses comparing the species composition of moth light trap catches from mown and unmown grasslands within the Kamenna trouba reserve.

	Axis1[a)]	Axis2[a)]	Axis3[a)]	Axis4[a)]	Total inertia[b)]	F, P axis 1[c)]	F, P all axes[c)]
Indirect PCA ordination							
Microlepidoptera	32.0	58.5	75.5	89.9	1.00		
Macolepidoptera	38.7	61.1	76.7	88.7	1.00		
Lepidoptera	35.8	57.4	73.0	87.0	1.00		
Direct CCA ordination, summed across all trapping nights							
Microlepidoptera	30.4	50.7	69.7	87.3	0.712	1.75***	
Macolepidoptera	35.8	26.4	74.3	88.1	0.609	2.23***	
Lepidoptera	25.8	45.8	65.4	83.6	0.787	1.39**	
Direct CCA ordination, trapping nights treated separately: site effect							
Microlepidoptera	2.6	4.5	6.2	7.7	5.297	2.60	0.92
Macrolepidoptera	3.4	5.3	6.9	8.1	3.494	1.68	0.97*
Lepidoptera	3.2	4.8	6.4	7.9	3.837	1.56	0.95
Direct CCA ordination, trapping nights treated separately: treatment effect							
Microlepidoptera	2.4	11.0	17.5	22.9	5.297	1.29***	
Macrolepidoptera	3.2	17.2	27.9	22.9	3.494	1.70**	
Lepidoptera	2.9	15.9	25.5	31.6	3.837	1.58***	

Explanations: [a)]Explained variation in moth catches, i.e., variation attributable to first four ordination axes; [b)] Eigenvalues of ordination axes are obtained as explained variation divided by total inertia; [c)] Based on Monte-Carlo permutation tests. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

analysing all species (Fig. 1), several humid grassland specialists associated with unmown conditions (e.g., *Clepsis spectrana*, *Macrochilo cribrumalis*, *Hypenodes humidalis*, *Simyra albovenosa*), while others associated with mown conditions (e.g., *Aethes cnicana*), and still others (e.g., *Cerapteryx graminis*, *Chortodes pygmina*) appeared as indifferent. It was also notable that traps from mown sections attracted migratory moths (e.g., *Noctua fimbriata*, *Xestia c-nigrum*) and moths associated with woody vegetation (e.g., *Smerinthus ocellatus*, *Biston betularia*). The same basic patterns appeared in separate analyses for Microlepidoptera and Macrolepidoptera (diagrams not shown).

The direct CCA ordinations corroborated the significant effect of management, corresponding with the first ordination axis, for all species, Microlepidoptera and Macrolepidoptera. On summed data, management explained ca 30% of the variation in species composition of catches, similarly to the indirect PCA analyses (Table 2). When reflecting the temporal aspect of the trapping, the variations explained were rather low, higher for Macrolepidoptera than for Microlepidoptera (Table 2), and again statistically significant. As in the PCAs, specialists ended up at various positions at the ordination space (Fig. 2). Some were associated with unmown conditions (Microlepidoptera: *Brachmia inornatella*, *Clepsis spectrana*; Macrolepidoptera: *Hypenodes humidalis*, *Macrochilo cribrumalis*); others with mown conditions (Microlepidoptera: *Aethes cnicana*, *Coleophora alticolella*), and still others appeared as indifferent (Microlepidoptera: *Glyphipterix thrasonella*, *Eudonia pallida*; Macrolepidoptera: *Cerapteryx graminis*, *Plusia putnami*). Contrary to Microlepidoptera, very few Macrolepidopteran specialists associated with mown conditions.

The above patterns were corroborated by χ^2 comparisons of the numbers of specialists associated positively, indifferently or negatively with mowing. Based on CCA ordination scores per individual species, the numbers of specialists preferring mowing, having no preference and preferring abandonment were 6, 16 and 19, i.e., the representation of specialists with these pref-

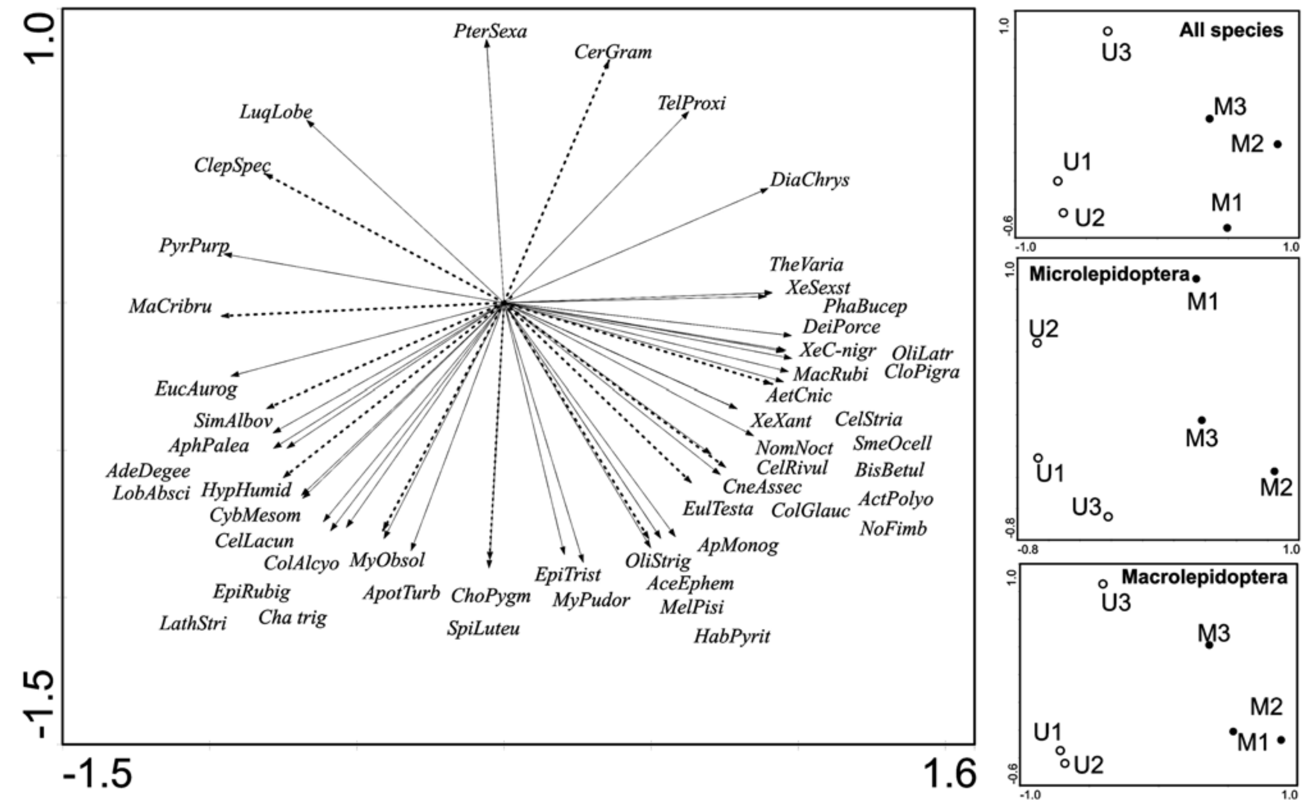

Fig. 1. Results of indirect (PCA) ordinations of light trap moth catches from mown and unmown sections of a humid grassland reserve. Left: scatterplot showing positions of individual species in relation to first and second ordination axes – analysis of all species, i.e. Microlepidoptera and Macrolepidoptera together. Only 51 species with a high (> 75%) fit are shown. Thicker dashed lines are used for humid grasslands specialists. Right: scatterplots showing positions of samples from mown (M1–M3) and unmown (U1–U3) sections in analyses of all Lepidoptera, and in separate analyses of Microlepidoptera and Macrolepidoptera. We see that the horizontal ordination axes, defined as the main gradient in variation in species composition of the moth catches, separate the mown and unmown sections of the grassland, corroborating the importance of mowing in structuring the moths community.
Key: *AceEphem – Acentria ephemerella, ActPolyo – Actinotia polyodon; AdeDegee – Adela degeerella; AetCnic – Aethes cnicana; AphPalea – Aphelia paleana; ApMonog – Apamea monoglypha; ApoTurb – Apotomis turbidana; BisBetul – Biston betularia; CelLacun – Celypha lacunana; CelRivul – C. rivulana; CelStria – Celypha striana; CerGram – Cerapteryx graminis; Chatrig – Charanyca trigrammica; ChoPygm – Chortodes pygmina; ClepSpec – Clepsis spectrana; CloPigra – Clostera pigra; CneAssec – Cnephasia asseclana; ColAlcyo – Coleophora alcyonipennella; ColGlauc – C. glaucicolella; CybMesom – Cybosia mesomella; DeiPorce – Deilephila porcellus; DiaChrys – Diachysia chrysitis; EpiRubig – Epinotia rubiginosana; EpiTrist – Epirrhoe tristata; EucAurog – Eucalybites auroguttellus; EulTesta – Eulithis testata; HabPyrit – Habrosyne pyritoides; HypHumid – Hypenodes humidalis; LathStri – Lathronympha strigana; LobAbsci – Lobesia abscisana; LuqLobe – Luquetia lobella; MaCribru – Macrochilo cribrumalis; MacRubi – Macrothylacia rubi; MelPisi – Melanchra pisi; MyObsol – Mythimna obsoleta; MyPudor – M. pudorina; NoFimb – Noctua fimbriata; NomNoct – Nomophila noctuella; OliLatr – Oligia latruncula; OliStrig – O. strigilis; PhaBucep – Phalera bucephala; PterSexa – Pterapherapteryx sexalata; PyrPurp – Pyrausta purpuralis; SimAlbov – Simyra albovenosa; SmeOcell – Smerinthus ocellatus; SpiLuteum – Spilosoma luteum; TelProxi – Teleiodes proximellus; TheVaria – Thera variata; XeC–nigr – Xestia c–nigrum; XeSext – X. sexstrigata; XeXant – Xestia xanthographa.*

erences did not differ from an even distribution ($\chi^2 = 4.27$, df = 2, $P = 0.12$). The same applied within Microlepidoptera (5, 6, 9; $\chi^2 = 0.94$, df = 2, $P = 0.63$) but not within Macrolepidoptera (1, 10, 9: $\chi^2 = 5.75$, df = 2, $P = 0.05$), in which more species preferred abandonment. Therefore, while most of humid grassland Macrolepidoptera preferred unmown conditions, microlepidopteran preferences were distributed evenly.

Discussion

Within a temperate fenland, moth catches from mown and unmown sections differed in the species composition of moth assemblages, pointing to the necessity of spatially diversified management for preserving a full biodiversity potential of grassland reserves (Morris 2000; Čížek et al. 2012). Moreover, the category of humid grassland specialists included species that preferred mowing, preferred abandonment, or displayed no preference at all.

It is easy to interpret the preferences of some specialists for unmown conditions. The noctuids *Hypenodes humidalis* and *Macrochilo cribrumalis* feed on decaying grass blades and hence prefer sections with high leaf litter accumulation, whereas the noctuids *Mythimna obsoleta* and *Chortodes minima* feed on tall grasses (*Phragmites australis* and *Deschampsia* spp., respectively) (Macek et al. 2008). The arctiid *Thumatha senex* feeds on mosses amids unmown grass tussocks (Macek et al. 2007). Even for some Microlepidoptera, the preference for unmown sections can be interpreted straightforwardly. The Cosmopterygidae species *Cos-*

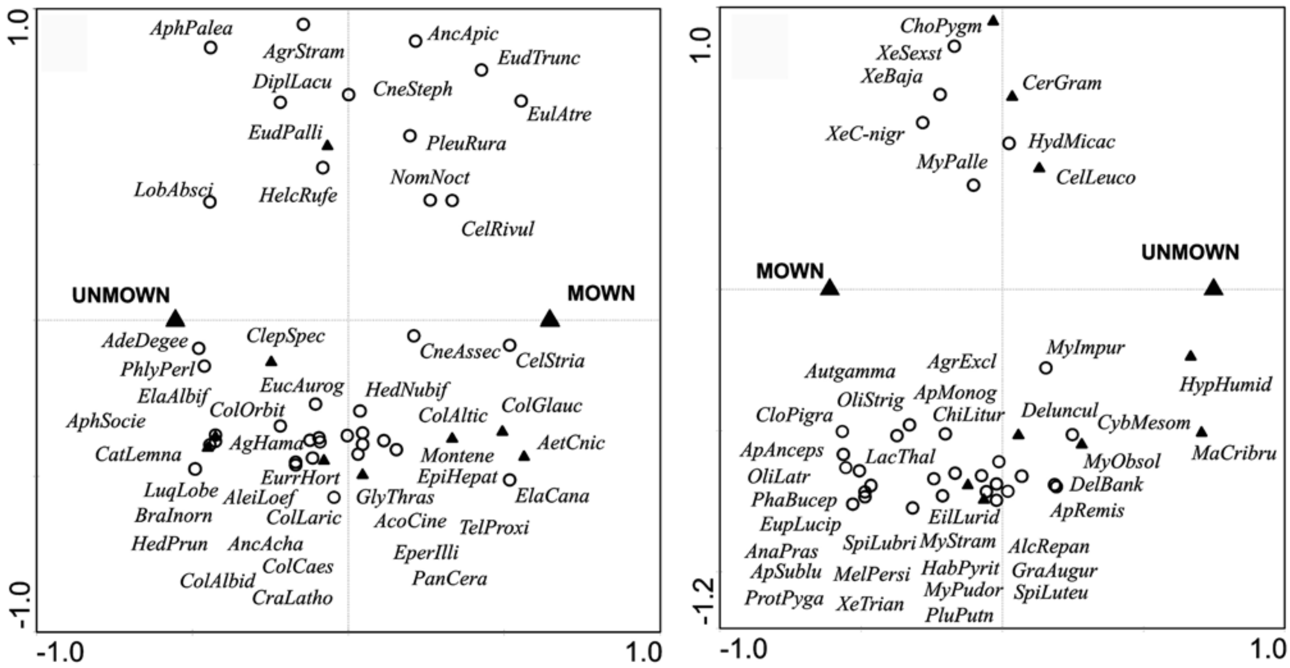

Fig. 2. Results of direct (CCA) ordinations relating the composition of light trap moth catches to management (mown vs. unmown: the large triangles stand for centroids of the two management effects) of a humid grassland. Results of separate analyses of a) Microlepidoptera and b) Macrolepidoptera. Dark triangles: humid grassland specialists; empty circles: remaining species. Only species with the highest fits to the models (> 20%) are shown. We see that whereas a majority of specialist Macrolepidoptera incline towards unmown sections, there are some specialist Microlepidoptera inclining towards the mown section as well.

Key – left panel. *AcoCine – Acompsia cinerella; AdeDegee – Adela degeerella;* AetCnic – *Aethes cnicana; AgHama – Agapeta hamana; AgrStram – Agriphila straminella; AleiLoef – Aleimma loeflingianum; AncAcha – Ancylis achatana; AncApic – A. apicella; AphPalea – Aphelia paleana; AphSocie – Aphomia sociella; BraInorn – Brachmia inornatella; CatLemna – Cataclysta lemnata; CelRivul – Celypha rivulana; CelStria – C. striana; ClepSpec – Clepsis spectrana; CneAssec – Cnephasia asseclana; ColAltic – Coleophora alticolella; ColCaes – C. caespititiella; ColGlau – C. glaucicolella; ColLaric – C. laricella; ColOrbit – C. orbitella;CraLatho – Crambus lathoniellus; DiplLacu – Dipleurina lacustrata; ElaAlbif – Elachista albifrontella; EperIlli – Epermenia illigerella; EpiHepat – Epiblema hepaticanum; EucAurog – Eucalybites auroguttellus; EudPalli – Eudonia pallida; EudTrunc – E. truncicolella; EulAtre – Eulamprotes atrella; EurrHort – Eurrhypara hortulatathras; GlyThras – Glyphipterix thrasonella; HedNubif – Hedya nubiferana; HedPrun – H. pruniana; HelcRufe – Helcystogramma rufescens; LobAbsci – Lobesia abscisana; LuqLobe – Luquetia lobella; Montene – Monochroa tenebrella; NomNoct – Nomophila noctuella; PanCera – Pandemis cerasana; PleuRura – Pleuroptya ruralis; TelProxi – Teleiodes proximellus.* Right panel: *AgrExcl – Agrotis exclamationis; AlcRepan – Alcis repandata; AnaPras – Anaplectoides prasinus; ApAnceps – Apamea anceps; ApMonog – A. monoglypha; ApRemis – A. remissa; ApSublu – A. sublustris; Autgamma – Autographa gamma; CelLeuco – Celaena leucostigma; CerGram – Cerapteryx graminis; ChiLitur – Chiasmia liturata; ChoPygm – Chortodes pygmina; CloPigra – Closter pigra; CybMesom – Cybosia mesomella; DelBank – Deltote bankiana; Deluncul – D. uncula; EilLurdi – Eilema lurideolum; EupLucip – Euplexia lucipara; HaPyrit – Habrosyne pyritoides; HydMicac – Hydraecia micacea; HypHumid – Hypenodes humidalis; GraAugur – Graphiphora augur; LacThal – Lacanobia thalassina; MaCribru – Macrochilo cribrumalis; MelPersi – Melanchra persicariae; MyImpur – Mythimna impura; MyObsol – M. obsoleta; MyPalle – M. pallens; MyPudor – M. pudorina; MyStramin – M. straminea; OliLatru – Oligia latruncula; OliStrig – Oligia strigilis; PhaBucep – Phalera bucephala; PluPutn – Plusia putnami; ProtPyga – Protodeltote pygarga; SpiLubri – Spialia lubricipeda; SpiLuteum – S. luteum; XeBaja – Xestia baja*; *XeCnigr – X. c-nigrum; XeSexst – X. sexstrigata; XeTrian – X. triangulum.*

mopterix lienigiella and *C. orichalcea* both develop on *Phragmites australis* (Koster & Sinev 2003), which does not tolerate mowing. Feeding on *Phragmites* also applies for the tortiricid *Brachmia inornatella*, whereas the tortricid *Clepsis spectrana* develops on multiple unrelated plants (e.g., *Scirpus lacustris*, *Comarum palustre*, *Glyceria spectabilis*, *Epilobium hirsutum*), which occur in damp waterlogged conditions (cf. Razowski 2001).

Explaining the preference of some humid grassland specialists for mown conditions is more difficult. Microlepidoptera, which contained more such specialists, included the tortricids *Bactra lancealana* developping on *Juncus* spp. and *Scripus* spp., and *Aethes cnicana* requiring *Cirsium* spp. seedheads for larvae (cf. Razowski 2001). Several species showing this preference are rather typical for damp fens, e.g. the colephorids *Coleophora glaucicolella* and *C. alticolella*, both feeding on *Juncus* spp. (Emmet et al. 1996), or the tortricid *Phalonidia manniana* feeding on emerged macrophytes, such as *Mentha* spp. or *Alisma plantago-aquatica* (Razowski 2001). The only macrolepidopteran representative, the noctuid *Archanara sparganii*, normally feeds on tall watery plants, such as *Sparganium* spp., and hence should not tolerate mowing (Macek et al. 2008). It was, however, captured in a low total number ($n = 4$), contrasting with the macrolepidopteran specialists inclining towards unmown sections (e.g., *Hypenodes humidalis*: 54, *Mythimna obsoleta*: 35). In some species, perhaps, the affinity towards mown conditions was due to preference for specific host plant's physiological state (e.g., graminoid leaves resprouting after cuts are more nutritious than old leaves: Čížek 2005), or because some host plant species were underrepresented at unmown sections due to increased competition.

On the other hand, many Macrolepidoptera displaying affinity for mown sections were common grassland generalists (e.g., *Oligia latruncula*) and migrating moths (e.g., *Xestia c-nigrum*). A notable habitat sensitive (although not classified as a specialist) macrolepidopteran moth showing a much higher abundance at mown sections ($n = 183$, vs. 44 at unmown sextions) was *Xestia sexstrigata*, a regionally rare noctuid associated with humid flower-rich grasslands (Macek et al. 2008). The higher frequencies of all these species at mown sections could have been due to temporarily enhanced supplies of such resources as nectar, which gets scarcer at unmown meadows, but becomes plentiful as mown meadows later in season, when such species are flying, Plus, some of the moths trapped mainly at mown sections were likely immigrants from nearby biotopes (e.g., *Thera variata* develops on conifers, *Clostera pigra* and *Phalera bucephala* are associated with deciduous trees), suggesting an effect of better visibility of the traps in shorter sward, resulting into higher attraction of moths from larger distances, compared to unmown conditions.

Microlepidoptera versus Macrolepidoptera

The proportion of variation attributable to management was consistently higher for Macrolepidoptera in all ordination tests. This was somehow surprising, as we expected a lower mobility and a tighter dependency on specific habitat features such as host plant (cf. Loder et al. 1998), and hence more direct responses to management, in Microlepidoptera. Lower Microlepidoptera mobility, and higher specialisation and sensitivity, however, are only poorly supported in literature. The few existing autecological studies (e.g., Menendez & Thomas 2000) suggest that while this may be so for some species, it hardly represents a general rule. It is more likely that Microlepidoptera cover as diverse an array of life histories (cf. Gaston et al. 1992) as do Macrolepidoptera (Gaston & Reavey 1989).

Still, several species, mainly Microlepidotera, displayed an association with mown sections. Had we based our analysis on Macrolepidoptera only, the overwhelming preference of almost all specialists for unmown conditions would lead us to conclude that mowing should be restricted to a minimum necessary to prevent woody encroachement. Inclusion of Microlepidoptera revealed that some humid grassland specialists profit from regular mowing as well.

Conservation implications

As in other arthropod groups (e.g., Balmer & Erhardt 2000; Kruess & Tscharntke 2002; Woodcock et al. 2005, 2007; Sjodin et al. 2008), preserving maximum local moth diversity requires grassland cuts to vary in extent and intensity. Due to individualistic (Bourn & Thomas 2002) and often not precisely known species requirements, it is impossible to design a cutting strategy that would perfectly suit all species present at each site. As convincingly argued by Dennis et al. (2003, 2010), and others (e.g., Vanreusel & Van Dyck 2007), the components of arthropod habitats, including larval and adult food, shelter, roosting and mating sites, etc., may occur disjunctly in time and space. In terms of ecosystem dynamics, the coexistence of diverse species assemblages results from interplays of patchily occurring disturbances followed by succession (Wu & Loucks 1995), to which species adapt via dynamic metapopulation processes (Aviron et al. 2007). In cultural landscapes, including highlands of Central Europe, natural ecosystem processes were replaced by traditional small-scaled farming, allowing species to track momentarily suitable conditions. Realising the biodiversity potential of small reserves embedded within homogenised, intensively cultivated modern landscapes thus requires providing a maximum variety of resources located in close proximity.

It is rather surprising that this common-sense knowledge has evaded conservation managers for such a long time. Too often, grassland reserves are managed uniformly, partly for practical considerations (e.g., it is cheaper to cut a whole reserve at once than to maintain a mosaic of temporarily mown and unmown sections), and partly due to poor understanding by managers (Waring 2001; Konvička et al. 2008).

Temporary abandonment spanning for several seasons is an illustrative case. Although it demonstrably benefits some valuable species, particularly those associated with leaf litter (such as *Hypenodes humidalis* and *Macrochilo cribrumalis*), it is abhorred by reserve managers, who view it as contradictory to the traditional land uses that the reserves are supposed to maintain. However, as argued by Morris (2000), it does not suffice that management of small grassland reserves just mimics traditional land use, because in homogenised landscapes, existing reserves need to pack a maximum of the past biodiversity of wider landscapes. The current increasingly advocated practices such as rotational fallow (Schmidt et al. 2008), or strip-mowing with postponed cuts (Grill et al. 2008; Čížek et al. 2012) represent methods of including temporary abandonment to reserve management techniques.

Our observations from a single reserve can be expanded to non-protected farmlands as well. The findings that farming by smaller land use units positively influences species richness (Rundlöf & Smith 2006; Rundlöf et al. 2008), or that local biodiversity increases in proximity of such structures as hedgerows or grassy strips (Croxton et al. 2005; Kuussaari et al. 2007; Merckx et al. 2009b) partly because hedgerows are shelter-providing resources (Merckx et al. 2008, 2010) all reveal a crucial role of biotope heterogeneity (Benton et al. 2003; Schweiger et al. 2005). For non-protected grasslands, heterogeneity enhancement via diminishing land management units, establishing temporary fallows, or varying livestock densities, will always be beneficial. These considerations are crucial for lands subsiudised to promote biodiversity, such as those under EU agrienvironmental schemes. Scheme options that fail to promote structural heterogeneity should be revised by introducing simple heterogeneity-enhancing measures, in order to increase their biodiversity benefits.

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Appendix. Systematic list of species trapped to light traps during a light trapping study in the Kamenna trouba reserve, with abbreviations used in ordination diagrams, species fits in the CCA ordination models testing responses of the moth assemblages to mowing, and total numbers captured at the mown and unmown sections.

Family, species	Specialist	Axis 1 score	Axis 2 score	Total umnown	Total mown
Hepialidae					
Hepialus sylvinus (L., 1761)		–0.2767	–0.6536		3
Nepticulidae					
Ectoedemia albifasciella (Heinemann, 1871)		–0.6171	–0.6729		1
Opostegidae					
Opostega salaciella (Treitschke, 1833)		–0.6171	–0.2518		1
Pseudopostega crepusculella (Zeller, 1839)	+	–0.6171	–0.3485		1
Adelidae					
Adela degeerella (L., 1758)		0.9062	–0.7085	5	
Incurvariidae					
Incurvaria oehlmanniella (Hübner, 1796)		–0.2519	–0.0274	1	2
Bucculatricidae					
Bucculatrix ulmella Zeller, 1848		–0.6171	–0.5717		1
Gracillariidae					
Caloptilia elongella (L., 1761)		0.6776	–0.4317	1	
Caloptilia stigmatella (F., 1781)		0.6776	–0.0915	1	
Eucalybites auroguttellus (Stephens, 1835)		0.2824	–0.9624	44	13
Calybites phasianipennellus (Hübner, 1813)		0.4259	–0.6711	30	9
Leucospilapteryx omissella (Stainton, 1848)		0.1715	–0.2966	2	1
Parornix fagivora (Frey, 1861)		0.0302	–0.6306	1	1
Parornix devoniella (Stainton, 1850)		–0.6924	–0.7956		2
Parornix finitimella (Zeller, 1850)		–0.6171	–0.2473		1
Phyllonorycter froelichiellus (Zeller, 1839)		–0.6171	–0.4919		1
Yponomeutidae					
Yponomeuta evonymellus (L., 1758)		–0.6171	0.5462		1
Yponomeuta sedellus Treitschke, 1832		–0.6171	0.5462		1
Swammerdamia caesiella (Hübner, 1796)		0.6776	–0.5899	1	
Argyresthia glabratella (Zeller, 1847)		–0.6171	–0.2473		1
Argyresthia brockeella (Hübner, 1813)		–0.6171	–0.2518		1
Argyresthia goedartella (L., 1758)		–0.6171	0.4622		1
Argyresthia spinosella Stainton, 1849		0.6776	–0.7985	1	
Argyresthia pruniella (Clerck, 1759)		0.6776	–0.0915	1	
Plutellidae					
Plutella xylostella (L., 1758)		0.1289	–0.7857	7	6
Glyphipterigidae					
Glyphipterix thrasonella (Scopoli, 1763)	+	0.0302	–0.9432	2	2
Ethmiidae					
Ethmia quadrillella (Goeze, 1783)		0.6776	–0.659	1	
Depressariidae					
Luquetia lobella (Den. & Schiff., 1775)		0.9259	–1.1484	9	
Agonopterix arenella (Den. & Schiff., 1775)		–0.6924	–0.6826		2
Depressaria daucella (Den. & Schiff., 1775)		–0.8553	1.1488		9
Depressaria chaerophylli Zeller, 1839		0.0302	–0.1379	1	1
Elachistidae					
Elachista albifrontella (Hübner, 1817)		0.8163	–0.829	2	
Elachista pomerana (Frey, 1870)		0.3124	–0.7668	2	1
Elachista canapennella (Hübner, 1813)		–0.7558	–0.7119		2
Elachista maculicerusella Bruand, 1859	+	0.1179	–0.5498	9	7
Coleophoridae					
Coleophora spinella (Schrank, 1802)		–0.6171	–0.3485		1
Coleophora orbitella Zeller, 1849		0.4704	–0.9903	3	1
Coleophora alcyonipennella (Kollar, 1832)		0.3786	–0.6339	7	2
Coleophora mayrella (Hübner, 1813)		0.0302	–0.2416	1	1
Coleophora albidella (Den. & Schiff., 1775)		0.2981	–1.0827	9	2
Coleophora laricella (Hübner, 1817)		0.1832	–1.0359	67	71
Coleophora caespititiella Zeller, 1839	+	0.2376	–1.0625	11	7
Coleophora glaucicolella Wood, 1892	+	–0.7154	–0.8226	5	55
Coleophora alticolella Zeller, 1849	+	–0.4477	–1.2169	4	19
Coleophora sternipennella (Zetterstedt, 1839)		0.0302	–0.9687	1	1
Coleophora striatipennella Tengström, 1848		0.0604	–0.9763	10	9
Blastobasidae					
Hypatopa binotella (Thunberg, 1794)		0.8466	–0.2827	3	
Cosmopterigidae					
Cosmopterix orichalcea Stainton, 1861	+	0.6776	–0.4317	1	
Cosmopterix lienigiella Lienig & Zeller, 1846	+	0.7528	–0.9358	2	
Gelechiidae					
Monochroa tenebrella (Hübner, 1817)		0.0547	–1.025	15	18
Monochroa conspersella (Her.-Sch., 1854)	+	0.0030	–0.7558	9	13
Monochroa lutulentella (Zeller, 1839)		0.6776	0.7265	1	

Appendix (continued)

Family, species	Specialist	Axis 1 score	Axis 2 score	Total umnown	Total mown
Eulamprotes atrella (Den. & Schiff., 1775)		–0.8163	0.294		3
Bryotropha terrella (Den. & Schiff., 1775)		0.0302	–0.6662	1	1
Exoteleia dodecella (L., 1758)		0.1146	–1.0665	3	2
Teleiodes luculellus (Hübner, 1813)		0.0302	–1.0954	1	1
Teleiodes fugitivellus (Zeller, 1839)		–0.6171	–0.8706		1
Teleiodes proximellus (Hübner, 1796)		–0.1502	–1.1035	2	3
Teleiopsis diffinis (Haworth, 1828)		0.7528	–0.9358	2	
Chionodes tragicellus (Heyden, 1865)		–0.6171	1.0890		1
Chionodes electellus (Zeller, 1839)		–0.6171	–0.3485		1
Euscrobipalpa ocellatella (Boyd, 1858)		0.6776	–0.1027	1	
Brachmia inornatella (Douglas, 1850)	+	0.8575	–0.9901	33	1
Helcystogramma lutatellum (Her.-Sch., 1854)		0.8163	0.9866	2	
Helcystogramma rufescens (Haworth, 1828)		0.2429	–0.1624	7	5
Acompsia cinerella (Clerck, 1759)		0.0302	–0.8536	2	2
Limacodidae					
Apoda limacodes (Hufnagel, 1766)		0.6776	–0.4317	1	
Zygaenidae					
Adscita statices (L., 1758)		–0.6171	–0.6729		1
Tortricidae					
Phalonidia manniana (Fischer v.R., 1839)	+	–0.6171	–0.2518		1
Agapeta hamana (L., 1758)		0.3124	–1.1326	2	1
Agapeta zoegana (L., 1767)		0.6776	0.8347	1	
Aethes smeathmanniana (F., 1781)		–0.1110	0.8258	1	2
Aethes cnicana (Westwood, 1854)	+	–0.8326	–0.9748		4
Aleimma loeflingianum (L., 1758)		0.3882	–0.9291	3	1
Acleris shepherdana (Stephens, 1852)	+	0.6776	0.8347	1	
Acleris aspersana (Hübner, 1817)		–0.2519	0.8948	1	2
Neosphaleroptera nubilana (Hübner, 1799)		–0.6171	–0.6729		1
Cnephasia stephensiana (Doubleday, 1849)		0.1059	0.1022	9	6
Cnephasia asseclana (Den. & Schiff., 1775)		–0.2428	–0.6756	14	40
Cnephasia genitalana Pierce & Metcalfe, 1922		–0.8163	0.6259		3
Eulia ministrana (L., 1758)		0.0302	–0.6179	1	1
Argyrotaenia ljungiana (Thunberg, 1797)		–0.6171	–0.3485		1
Ptycholomoides aeriferanus (Her.-Sch., 1851)		–0.6171	–0.3485		1
Pandemis cerasana (Hübner, 1786)		0.0302	–1.0024	3	3
Pandemis heparana (Den. & Schiff., 1775)		0.6776	0.6122	1	
Syndemis musculana (Hübner, 1799)		–0.6924	–0.6826		2
Aphelia paleana (Hübner, 1793)		0.8437	0.3124	33	1
Clepsis spectrana (Treitschke, 1830)	+	0.5187	–0.7161	45	9
Bactra lancealana (Hübner, 1799)	+	–0.2374	–0.3264	13	28
Endothenia quadrimaculana (Haworth, 1811)		0.2066	–0.4803	64	44
Apotomis turbidana Hübner, 1825		0.177	–0.7922	2	2
Apotomis capreana (Hübner, 1817)		–0.565	–0.0994	1	6
Hedya salicella (L., 1758)		–0.0848	–0.7905	8	15
Hedya nubiferana (Haworth, 1811)		0.0448	–0.9217	6	7
Hedya pruniana (Hübner, 1799)		0.8466	–0.9981	3	
Celypha rufana (Scopoli, 1763)		0.6776	0.8813	1	
Celypha striana (Den. & Schiff., 1775)		–0.7558	–0.6435		2
Celypha lacunana (Den. & Schiff., 1775)		0.203	–0.2993	113	70
Celypha rivulana (Scopoli, 1763)		–0.4483	–0.2597	2	10
Olethreutes umbrosanus (Freyer, 1842)		0.0302	–1.0954	1	1
Olethreutes micanus (Den. & Schiff., 1775)	+	–0.2519	0.2233	1	2
Olethreutes palustranus (Lienig & Zeller, 1846)		–0.6171	–0.3485		1
Pseudohermenias abietana (Fabricius, 1787)		–0.6171	–0.6729		1
Lobesia abscisana (Doubleday, 1849)		0.8466	–0.1757	3	
Epinotia ramella (L., 1758)		0.6776	1.0920	1	
Epinotia tenerana (Den. & Schiff., 1775)		–0.6171	–0.2473		1
Epinotia tedella (Clerck, 1759)		0.0302	–0.6794	1	1
Epinotia rubiginosana (Her.-Sch., 1851)		0.2585	–1.0095	3	2
Epinotia nanana (Treitschke, 1835)		0.0302	–1.0107	1	1
Eucosma cana (Haworth, 1811)		0.0302	0.597	2	2
Gypsonoma dealbana (Frölich, 1828)		0.0302	–0.9425	2	2
Epiblema foenellum (L., 1758)		0.6776	–0.4317	1	
Epiblema scutulanum (Den. & Schiff., 1775)		0.6776	–0.5899	1	
Epiblema hepaticanum (Treitschke, 1835)		–0.0832	–0.9592	3	5
Notocelia cynosbatella (L., 1758)		0.6776	–0.4317	1	
Notocelia uddmanniana (L., 1758)		0.6776	–0.5899	1	
Notocelia incarnatana (Hübner, 1800)		–0.6171	1.0890		1
Notocelia trimaculana (Haworth, 1811)		0.0302	–0.094	1	1
Rhyacionia pinivorana (Lienig & Zeller, 1846)		0.1715	–0.7838	2	1
Ancylis laetana (F., 1775)		–0.6171	–0.4919		1

Appendix (continued)

Family, species	Specialist	Axis 1 score	Axis 2 score	Total umnown	Total mown
Ancylis diminutana (Haworth, 1811)		0.6776	–0.6590	1	
Ancylis achatana (Den. & Schiff., 1775)		0.2640	–1.1175	7	4
Ancylis badiana (Den. & Schiff., 1775)		0.6776	0.8311	1	
Ancylis apicella (Den. & Schiff., 1775)		–0.2519	0.3805	1	2
Lathronympha strigana (F., 1775)		0.2025	–0.2943	89	29
Dichrorampha simpliciana (Haworth, 1811)		0.6776	–0.0915	1	
Epermeniidae					
Epermenia illigerella (Hübner, 1813)		0.1121	–0.9233	15	19
Epermenia falciformis (Haworth, 1828)		0.8646	–0.1899	4	
Pterophoridae					
Pyralidae					
Aphomia sociella (L., 1758)		0.8163	–0.9670	2	
Pyla fusca (Haworth, 1811)		–0.6171	–0.4919		1
Acrobasis consociella (Hübner, 1813)		–0.6171	–0.2473		1
Scoparia basistrigalis Knaggs, 1866		0.6776	–0.2207	1	
Scoparia ambigualis (Treitschke, 1829)		0.1146	–0.2101	3	2
Dipleurina lacustrata (Panzer, 1804)		0.4704	0.1321	3	1
Eudonia pallida (Curtis, 1827)	+	0.2182	0.1569	24	12
Eudonia murana (Curtis, 1827)		0.6776	0.6122	1	
Eudonia truncicolella (Stainton, 1849)		–0.6045	0.4861	1	6
Chilo phragmitellus (Hübner, 1810)		–0.0668	–0.0275	10	10
Chrysoteuchia culmella (L., 1758)		0.2066	–0.5089	36	22
Crambus lathoniellus (Zincken, 1817)		0.2589	–1.0252	176	80
Crambus perlellus (Scopoli, 1763)		0.2443	–0.4037	8	4
Agriphila tristella (Den. & Schiff., 1775)		–0.2712	1.0493	3	6
Agriphila selasella (Hübner, 1813)		–0.3898	1.1863	3	15
Agriphila straminella (Den. & Schiff., 1775)		0.3477	0.8279	21	14
Agriphila geniculea (Haworth, 1811)		0.0302	1.0528	1	1
Catoptria margaritella (Den. & Schiff., 1775)		–0.6171	0.9878		1
Catoptria falsella (Den. & Schiff., 1775)		–0.6171	0.5462		1
Donacaula forficellus (Thunberg, 1794)	+	0.2554	0.4637	3	1
Elophila nymphaeata (L., 1758)	+	0.8163	–0.0049	2	
Acentria ephemerella (Den. & Schiff., 1775)	+	–0.2499	–0.4959	16	40
Cataclysta lemnata (L., 1758)	+	0.8163	–0.7556	2	
Udea ferrugalis (Hübner, 1796)		0.6776	–0.0155	1	
Udea prunalis (Den. & Schiff., 1775)		–0.6171	0.8311		1
Ecpyrrhorrhoe rubiginalis (Hübner, 1796)		0.6776	–0.0155	1	
Pyrausta purpuralis (L., 1758)		0.8768	0.5863	3	
Phlyctaenia coronata (Hufnagel, 1767)		0.8163	–0.4958	2	
Phlyctaenia perlucidalis (Hübner, 1809)		0.8768	–0.7609	3	
Eurrhypara hortulata (L., 1758)		0.3882	–0.8820	3	1
Pleuroptya ruralis (Scopoli, 1763)		–0.2217	0.4376	5	10
Nomophila noctuella (Den. & Schiff., 1775)		–0.3298	0.3892	5	16
Lasiocampidae					
Macrothylacia rubi (L., 1758)		–0.8457	–0.8314		5
Dendrolimus pini (L., 1758)		–0.2767	–0.6536	3	9
Sphingidae					
Sphinx pinastri L., 1758		–0.1502	–0.1816	2	3
Smerinthus ocellatus (L., 1758)		–0.7558	–0.4420		2
Laothoe populi (L., 1758)		0.2495	0.2875	6	3
Deilephila elpenor (L., 1758)		–0.6171	–0.5717		1
Deilephila porcellus (L., 1758)		–0.8163	–0.7844		3
Drepanidae					
Drepana falcataria (L., 1758)		0.8163	0.4699	2	
Watsonalla binaria (Hufnagel, 1767)		–0.6171	0.9878		1
Thyatira batis (L., 1758)		0.6776	–0.5899	1	
Habrosyne pyritoides (Hufnagel, 1766)		–0.3821	–0.6428	6	19
Tethea or (Den. & Schiff., 1775)		–0.6171	–0.6729		1
Ochropacha duplaris (L., 1761)		–0.7558	–0.5793		2
Geometridae					
Abraxas sylvatus (Scopoli, 1763)		0.6776	–0.0915	1	
Lomaspilis marginata (L., 1758)		0.8163	–0.2716	2	
Chiasmia notata (L., 1758)		–0.6171	0.8311		1
Chiasmia alternata (Den. & Schiff., 1775)		0.0302	0.1605	1	1
Chiasmia signaria (Hübner, 1809)		0.3124	–0.3698	2	1
Chiasmia liturata (Clerck, 1759)		–0.0882	–0.6389	7	9
Chiasmia clathrata (L., 1758)		–0.0412	0.2582	17	21
Chiasmia brunneata (Thunberg, 1784)		0.0302	–0.8460	1	1
Tephrina arenacearia (Den. & Schiff., 1775)		0.6776	–0.3109	1	
Plagodis pulveraria (L., 1758)		–0.6171	–0.4919		1
Ennomos alniarius (L., 1758)		–0.6924	0.8832		2

Appendix (continued)

Family, species	Specialist	Axis 1 score	Axis 2 score	Total umnown	Total mown
Odontopera bidentata (Clerck, 1759)		–0.6171	–0.4919		1
Biston betularius (L., 1758)		–0.8502	–0.5091		4
Peribatodes secundarius (Den. & Schiff., 1775)		–0.6171	0.6444		1
Alcis repandata (L., 1758)		–0.0423	–0.5678	5	7
Hypomecis punctinalis (Scopoli, 1763)		0.6776	–0.4317	1	
Ectropis crepuscularia (Den. & Schiff., 1775)		0.4704	0.6321	3	1
Aethalura punctulata (Den. & Schiff., 1775)		–0.6924	–0.5643		2
Ematurga atomaria (L., 1758)		–0.6171	0.2409		1
Bupalus piniarius (L., 1758)		0.6776	–0.6590	1	
Cabera exanthemata (Scopoli, 1763)		0.5177	0.3122	4	1
Lomographa temerata (Den. & Schiff., 1775)		0.6776	–0.0155	1	
Hylaea fasciaria (L., 1758)		0.6776	–0.5899	1	
Siona lineata (Scopoli, 1763)		–0.0711	–0.7849	4	4
Geometra papilionaria (L., 1758)		–0.1097	0.0888	2	4
Cyclophora albipunctata (Hufnagel, 1767)		–0.6171	0.9878		1
Cyclophora punctaria (L., 1758)		–0.6171	0.9878		1
Timandra comae Schmidt, 1931		0.1506	0.6088	6	5
Scopula immorata (L., 1758)		–0.313	0.2027	3	7
Scopula ornata (Scopoli, 1763)		–0.6171	0.8208		1
Scopula immutata (L., 1758)	+	–0.0673	0.3648	3	3
Idaea dimidiata (Hufnagel, 1767)		0.6776	0.5633	1	
Scotopteryx chenopodiata (L., 1758)		0.0302	1.0876	2	2
Orthonama vittata (Borkhausen, 1794)	+	0.2059	0.2385	36	35
Xanthorhoe biriviata (Borkhausen, 1794)		–0.6171	–0.2473		1
Xanthorhoe designata (Hufnagel, 1767)		–0.6171	–0.4657		1
Xanthorhoe spadicearia (Den. & Schiff., 1775)		–0.4433	0.1275	3	9
Xanthorhoe ferrugata (Clerck, 1759)		0.6416	0.395	5	1
Xanthorhoe quadrifasciata (Clerck, 1759)		–0.6171	–0.2473		1
Xanthorhoe montanata (Den. & Schiff., 1775)		–0.111	–0.5883	1	2
Catarhoe rubidata (Den. & Schiff., 1775)		–0.6171	–0.3485		1
Epirrhoe tristata (L., 1758)		–0.1798	–0.7903	3	6
Epirrhoe alternata (Müller, 1764)		0.3124	–0.7668	15	9
Camptogramma bilineatum (L., 1758)		–0.41	1.084	1	3
Eulithis testata (L., 1761)	+	–0.2966	0.9964	4	7
Eulithis populata (L., 1758)		0.3124	–0.5637	2	1
Eulithis pyraliata (Den. & Schiff., 1775)		0.6776	–0.0155	1	
Ecliptopera silaceata (Den. & Schiff., 1775)		–0.6171	0.8791		1
Ecliptopera capitata (Her.-Sch., 1839)		0.6776	–0.5899	1	
Chloroclysta truncata (Hufnagel, 1767)		–0.2519	–0.1615	1	2
Plemyria rubiginata (Den. & Schiff., 1775)		–0.6171	–0.2473		1
Thera firmata (Hübner, 1822)		–0.6924	0.7281		2
Thera obeliscata (Hübner, 1787)		–0.4100	0.2548	1	3
Thera variata (Den. & Schiff., 1775)		–0.8963	0.0720		8
Colostygia pectinataria (Knoch, 1781)		–0.1166	–0.0960	2	2
Hydriomena furcata (Thunberg, 1784)		0.0302	0.1430	1	1
Hydriomena impluviata (Den. & Schiff., 1775)		0.1146	–0.6159	3	2
Rheumaptera undulata (L., 1758)		0.6776	–0.0915	1	
Euphyia unangulata (Haworth, 1809)		0.1747	–0.1816	3	3
Perizoma alchemillatum (L., 1758)		–0.0916	0.1451	10	11
Eupithecia linariata (Den. & Schiff., 1775)		–0.6171	0.6922		1
Eupithecia tantillaria Boisduval, 1840		0.6776	–0.3109	1	
Eupithecia centaureata (Den. & Schiff., 1775)		–0.2519	0.2745	1	2
Eupithecia satyrata (Hübner, 1813)		–0.4572	–0.8681	1	4
Eupithecia absinthiata (Clerck, 1759)		–0.6171	0.4622		1
Eupithecia subumbrata (Den. & Schiff., 1775)		–0.6924	–0.7956		2
Chloroclystis v-ata (Haworth, 1809)		–0.6171	–0.3485		1
Rhinoprora rectangulata (L., 1758)		–0.6171	–0.2473		1
Euchoeca nebulata (Scopoli, 1763)		0.0302	–0.4237	1	1
Lobophora halterata (Hufnagel, 1767)		0.6776	–0.3109	1	
Pterapherapteryx sexalata (Retzius, 1783)				2	1
Notodontidae					
Clostera pigra (Hufnagel, 1766)		–0.9051	–0.1708		9
Furcula bicuspis (Borkhausen, 1790)		0.6776	0.5696	1	
Pheosia gnoma (F., 1776)		0.5614	0.5855		1
Pheosia tremula (Clerck, 1759)		–0.8229	1.0551		5
Ptilodon capucina (L., 1758)		–0.3891	–0.7758	1	4
Phalera bucephala (L., 1758)		–0.8868	–0.7206		9
Stauropus fagi (L., 1758)		–0.6171	–0.5717		1
Noctuidae					
Acronicta megacephala (Den. & Schiff., 1775)		–0.4100	–0.3706	1	3
Acronicta auricoma (Den. & Schiff., 1775)		–0.6171	0.6444		1

Appendix (continued)

Family, species	Specialist	Axis 1 score	Axis 2 score	Total umnown	Total mown
Acronicta rumicis (L., 1758)		0.6776	0.6122	1	
Simyra albovenosa (Goeze, 1781)	+	0.5103	0.4864	45	10
Macrochilo cribrumalis (Hübner, 1793)	+	0.9681	–0.3308	12	
Herminia tarsicrinalis (Knoch, 1782)		0.8163	–0.4915	2	
Polypogon tentacularius (L., 1758)		0.8163	–0.4468	2	
Hypenodes humidalis Doubleday, 1850	+	0.9109	–0.0275	53	1
Catocala nupta (L., 1767)		0.6776	0.5808	1	
Laspeyria flexula (Den. & Schiff., 1775)		0.0302	–0.2878	1	1
Scoliopteryx libatrix (L., 1758)		0.1715	–0.2427	2	1
Hypena proboscidalis (L., 1758)		–0.6171	0.5614		1
Rivula sericealis (Scopoli, 1763)		0.0918	0.2424	16	12
Macdunnoughia confusa (Stephens, 1850)		–0.6171	0.8208		1
Plusia festucae (L., 1758)	+	0.3124	0.9536	2	1
Plusia putnami (Grote, 1873)	+	–0.1664	–0.5767	5	9
Diachrysia chrysitis (L., 1758)		–0.5812	–0.2501	1	5
Autographa gamma (L., 1758)		–0.6206	–0.3434	1	7
Protodeltote pygarga (Hufnagel, 1766)		–0.8504	–0.6532		6
Deltote bankiana (F., 1775)		0.2021	–0.8382	30	16
Deltote uncula (Clerck, 1759)	+	0.0138	–0.5686	13	14
Deltote deceptoria (Scopoli, 1763)		0.4342	–1.0429	13	4
Trisateles emortualis (Den. & Schiff., 1775)		0.6776	–0.6590	1	
Amphipyra pyramidea (L., 1758)		–0.6171	0.6922		1
Amphipyra tragopoginis (Clerck, 1759)		0.8163	0.8126	2	
Heliothis armigera (Hübner, 1808)		0.0302	1.0729	1	1
Elaphria venustula (Hübner, 1790)		0.349	–0.6962	3	2
Caradrina morpheus (Hufnagel, 1766)		0.0302	–0.3030	1	1
Hoplodrina octogenaria (Goeze, 1781)		0.0425	–0.0084	7	9
Hoplodrina blanda (Den. & Schiff., 1775)		–0.3759	–0.4228	1	4
Charanyca trigrammica (Hufnagel, 1766)		0.3243	–0.7989	31	6
Dypterygia scabriuscula (L., 1758)		–0.6171	–0.4919		1
Rusina ferruginea (Esper, 1785)		–0.1784	–0.5580	3	5
Euplexia lucipara (L., 1758)		–0.7558	–0.4438		2
Actinotia polyodon (Clerck, 1759)		–0.7558	–0.2829		2
Ipimorpha retusa (L., 1761)		0.6776	0.7265	1	
Enargia paleacea (Esper, 1788)		–0.7861	1.0924		3
Parastichtis suspecta (Hübner, 1817)		0.0302	0.1071	1	1
Parastichtis ypsillon (Den. & Schiff., 1775)		–0.7558	–0.3851		2
Cosmia trapezina (L., 1758)		–0.7558	0.5979		2
Antitype chi (L., 1758)		–0.6171	1.0209		1
Apamea monoglypha (Hufnagel, 1766)		–0.3675	–0.2489	2	5
Apamea sublustris (Esper, 1788)		–0.7861	–0.4646		3
Apamea crenata (Hufnagel, 1766)		–0.2519	–0.6650	1	2
Apamea remissa (Hübner, 1809)		0.2111	–0.7873	15	5
Apamea unanimis (Hübner, 1813)	+	–0.1502	–0.8976	2	3
Apamea anceps (Den. & Schiff., 1775)		–0.8163	–0.7681		3
Apamea sordens (Hufnagel, 1766)		0.0302	–0.5694	1	1
Oligia strigilis (L., 1758)		–0.3172	–0.9199	2	5
Oligia latruncula (Den. & Schiff., 1775)		–0.8995	–0.4241		11
Mesapamea secalis (L., 1758)		–0.6171	0.4622		1
Mesapamea didyma (Esper, 1788)		–0.6171	0.9519		1
Luperina testacea (Den. & Schiff., 1775)		–0.6171	0.9924		1
Amphipoea fucosa (Freyer, 1830)		0.2960	0.3815	25	18
Hydraecia micacea (Esper, 1789)		–0.0361	1.1091	25	25
Gortyna flavago (Den. & Schiff., 1775)		–0.0234	1.0513	4	5
Celaena leucostigma (Hübner, 1808)	+	0.1216	1.0193	56	44
Archanara sparganii (Esper, 1790)	+	–0.8326	0.9568		4
Chortodes minima (Haworth, 1809)	+	0.2403	0.2165	6	3
Chortodes fluxa (Hübner, 1809)		0.8768	0.8548	3	
Chortodes pygmina (Haworth, 1809)	+	–0.1184	1.2075	13	11
Discestra trifolii (Hufnagel, 1766)		–0.6171	0.8791		1
Lacanobia oleracea (L., 1758)		–0.2519	0.2107	1	2
Lacanobia contigua (Den. & Schiff., 1775)		0.6776	–0.3109	1	
Lacanobia thalassina (Hufnagel, 1766)		–0.4283	–0.5786	2	9
Lacanobia suasa (Den. & Schiff., 1775)		–0.1502	1.0293	2	3
Hada plebeja (L., 1761)	+	–0.2996	–0.7955	4	6
Hadena bicruris (Hufnagel, 1766)		–0.6171	–0.5717		1
Hadena luteago (Den. & Schiff., 1775)		0.6776	–0.2207	1	
Melanchra persicariae (L., 1761)		–0.7861	–0.4867		3
Melanchra pisi (L., 1758)		–0.2300	–0.9282	3	10
Mamestra brassicae (L., 1758)		–0.571	1.0404	2	12
Mythimna conigera (Den. & Schiff., 1775)		–0.6171	–0.3485		1

Appendix (continued)

Family, species	Specialist	Axis 1 score	Axis 2 score	Total umnown	Total mown
Mythimna albipuncta (Den. & Schiff., 1775)		0.3124	1.1814	2	1
Mythimna pudorina (Den. & Schiff., 1775)		–0.1015	–0.6249	21	30
Mythimna straminea (Treitschke, 1825)	+	–0.2508	–0.4033	2	4
Mythimna impura (Hübner, 1808)		0.1570	0.1957	123	109
Mythimna pallens (L., 1758)		–0.2209	0.6068	25	86
Mythimna obsoleta (Hübner, 1803)	+	0.3438	–0.8820	34	11
Mythimna comma (L., 1761)		–0.6171	–0.5717		1
Cerapteryx graminis (L., 1758)	+	–0.0201	1.2512	10	11
Tholera decimalis (Poda, 1761)		–0.3151	1.0182	4	12
Axylia putris (L., 1761)		0.4704	–0.5055	3	1
Ochropleura plecta (L., 1761)		–0.1030	0.4579	154	218
Diarsia brunnea (Den. & Schiff., 1775)		–0.1110	–0.3339	1	2
Diarsia rubi (Vieweg, 1790)	+	0.2147	0.2554	10	6
Noctua pronuba (L., 1758)		–0.2408	1.0885	3	5
Noctua comes Hübner, 1813		–0.3759	0.9661	1	4
Noctua fimbriata (Schreber, 1759)		–0.7558	0.2401		2
Noctua janthina Den. & Schiff., 1775		–0.6171	1.0209		1
Anaplectoides prasinus (Den. & Schiff., 1775)		–0.7861	–0.4867		3
Graphiphora augur (F., 1775)		0.0302	–0.3768	2	2
Eugraphe sigma (Den. & Schiff., 1775)		0.6776	–0.0155	1	
Eugnorisma glareosa (Esper, 1788)		–0.6171	1.0209		1
Xestia c-nigrum (L., 1758)		–0.4859	0.9503	35	247
Xestia ditrapezium (Den. & Schiff., 1775)		0.0874	–0.0678	9	9
Xestia triangulum (Hufnagel, 1766)		–0.5388	–0.7336	5	25
Xestia baja (Den. & Schiff., 1775)		–0.3949	1.2126	8	22
Xestia rhomboidea (Esper, 1790)		–0.6171	0.6173		1
Xestia sexstrigata (Haworth, 1809)		–0.3202	1.2744	43	183
Xestia xanthographa (Den. & Schiff., 1775)		–0.7558	0.9580		2
Naenia typica (L., 1758)		0.0302	–0.2416	1	1
Agrotis ipsilon (Hufnagel, 1766)		–0.2519	1.1067	1	2
Agrotis exclamationis (L., 1758)		–0.555	–0.5115	2	13
Agrotis segetum (Den. & Schiff., 1775)		–0.2519	1.0311	1	2
Lymantriidae					
Calliteara pudibunda (L., 1758)		0.0302	–0.5694	1	1
Euproctis chrysorrhoea (L., 1758)		–0.6171	–0.2473		1
Nolidae					
Pseudoips prasinanus (L., 1758)		–0.7861	–0.7618		3
Earias clorana (L., 1761)		0.6776	–0.3109	1	
Arctiidae					
Thumatha senex (Hübner, 1808)	+	0.4128	0.0312	12	5
Cybosia mesomella (L., 1758)		0.2947	–0.1483	24	6
Atolmis rubricollis (L., 1758)		–0.6171	–0.2518		1
Eilema lutarellum (L., 1758)		–0.6171	0.5614		1
Eilema complanum (L., 1758)		–0.4654	0.2599	2	6
Eilema lurideolum (Zincken, 1817)		–0.1536	–0.4454	6	9
Eilema depressum (Esper, 1787)		0.0302	0.5952	1	1
Spilosoma lubricipeda (L., 1758)		–0.1799	–0.9697	11	18
Spilosoma luteum (Hufnagel, 1766)		–0.1009	–0.5164	5	4
Phragmatobia fuliginosa (L., 1758)		–0.0772	0.5645	29	33
Arctia caja (L., 1758)		–0.2039	0.8739	15	26
Diacrisia sannio (L., 1758)		–0.1905	–0.3145	8	16