



Traits in Lepidoptera assemblages are differently influenced by local and landscape scale factors in farmland habitat islands

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Abstract: Semi-natural grassland islands have a key role in slowing down biodiversity decline in intensively cultivated agricultural landscapes. Assemblages in such habitat patches are not only limited by local habitat quality, but are also influenced by the suitability and distribution of different habitat types in the surrounding landscape. If we want to preserve a functionally diverse Lepidoptera fauna, both local and landscape scale environmental effects, including land use and management, should be considered. In the present study, we describe trait-based characteristics of noctuid dominated macro-moth assemblages (MMAs) in grassland remnants of an intensively cultivated agricultural area. By gathering environmental data from local to landscape scales, we aimed to identify the most influential scales, possible interactions between scales and the role of integrated arable fields in shaping MMAs. We conducted abundance weighted trait-based multivariate analysis of the assemblages based on six trait groups. Both local and landscape scale variables had important influence, acting on different traits of the assemblages. By variance partitioning, we could identify variables that exerted maximal effect at 50 m and 250 m radii circles. Variables describing local vegetation and identity of neighbouring crop were responsible for species richness and rarity status, while the area of arable and wooded habitats within 250 m were responsible for total catch and pest status related traits. There was significant interaction between principal components axes representing local and landscape variables. Rarity, more than other traits, was influenced by the interaction. Integrated fields had no effect on MMAs. The present study highlights the contributions of both local and landscape scales to the shaping of MMAs and suggests that the preservation of both local habitat quality and landscape heterogeneity are important if we would like to maintain species rich and functionally diverse Lepidoptera fauna.

Abbreviations. AES–Agri-Environmental Schemes; AES_Arabl–Arable fields in AES; Arabl–Arable fields; HumBott–Bottom Humidity; Meadw–Meadow habitats; MMA–noctuid dominated Macro-Moth Assemblage; NBcrop–Neighbouring crop; NBRic–Neighbourhood Richness; Physgn–Physiognomy; Shrub–Shrub dominance; Slope–Slope steepness; South–Southern exposition; SpecNumb–Number of Species; TotCatch–Total number of individuals caught; VegHgh–Vegetation Height; VegRic–Vegetation Richness; Wetl–Wetland; wMobil–abundance weighted Mobility score; Wood–Wooded habitats; wPest–abundance weighted Pest status score; wSize–abundance weighted body Size score; wVoltin–abundance weighted Voltinism score.

Introduction

Land use intensification threatens natural communities in agricultural landscapes (Benton et al. 2002). In intensively cultivated agricultural areas, habitat fragments generally shrunk to small islands of semi-natural habitats. However, even such small patches of semi-natural areas, such as grasslands, among cropland may serve as refuge for many plant and animal groups and contribute to the preservation of biodiversity (Saunders et al. 1991, Fischer and Lindenmayer 2007). These processes are in the forefront of landscape ecology research, with many papers documenting biodiversity loss for various components of the biota (Biesmeijer et al. 2006, van Swaay et al. 2006, Butler et al. 2010), and others dealing with how various land use practices could mitigate

these effects (Gonthier et al. 2014, Tuck et al. 2014). Among other measures, agri-environmental schemes (AES) in the European Union were implemented to reverse the decline of biodiversity, making farmers interested in changing farming practices in variable ways beneficial for the environment. These measures typically involve field extensification, diversification of landscape elements and local habitats (Kleijn and Sutherland 2003).

Lepidoptera, especially butterflies, are currently a focal group for studying the possibilities to conserve insect communities and the ecosystem services they provide in European landscapes. A large number of recent studies deal concurrently with local, habitat scale effects and landscape scale effects, but with different focus. These studies identified key habitat and landscape components that exerted effects on

Lepidoptera communities, such as the importance of habitat level resources (Thomas et al. 2001, Heikkinen et al. 2005), habitat area (Krauss et al. 2003, Öckinger and Smith 2006) and – usually in combination with local factors – landscape complexity and configuration (Öckinger and Smith 2006, Slancarova et al. 2014, Kormann et al. 2015). The majority of papers consider species richness or some form of diversity measure as the key descriptor of the community (Krauss et al. 2003, Rundlöf and Smith 2006, Ekroos and Kuussaari 2012, Öckinger et al. 2012, Liivamagi et al. 2014), others analyse community composition (Grand and Mello 2004, Meehan et al. 2013) and recently a number of studies use trait-based descriptors (Ekroos et al. 2010, Jonason et al. 2012, Kormann et al. 2015, Perović et al. 2015).

If we want to optimize conservation measures and give recommendations on how land use could be changed in the most effective way to stop, or at least slow down the decline of insect communities, then an explicit scale-dependent approach is necessary which identifies effective distances for any such measures. Variation partitioning methods allow us to decompose the amount of variance in a community explained by the spatial scales where environmental variables are determined (Borcard et al. 1992). This technique enables the examination of specific habitat characteristics that are most correlated with community characteristics at each level. Such techniques have been used in studying the distribution of single species lepidopteran populations (Heikkinen et al. 2005), and species composition in lepidopteran communities (Grand and Mello 2004). However, assemblages of species rich taxa, such as those of Lepidoptera, encompass functionally diverse set of species, thus a trait-based approach to uncover assemblage – environment relationships is more promising than treating all species equal (Violle et al. 2007). When linking species traits to the functioning of ecosystems, species abundance is an important measure (Gagic et al. 2015). Therefore, we regard that the relationship of assemblages to the environment are best captured by a trait-based approach, where traits are weighted by species abundance.

The present study describes the abundance weighted trait-based characteristics of noctuid dominated macro-moth assemblages (MMAs) in grassland remnants of an intensively cultivated agricultural area. By gathering environmental data from the local to the landscape scales at 9 different levels, we ask: (i) What are the prominent features at each scale that influence MMAs? (ii) What is the relative importance of each scale, measured by their unique contribution in the explanation of MMAs? (iii) Is there any interaction between local and landscape scale effects? (iv) Does the presence of AES arable fields in the landscape make a difference for the assemblages?

Materials and methods

Study area and descriptive variables

Sites. Our research was conducted in 14 geographically distinct grassland patches (closest distance between patches was 1 km, largest distance was 69 km), in the Mezőföld region,

Hungary. The Mezőföld, laying west to the river Danube, is an elevated loess plateau with average height of 150 m a.s.l. During the Ice Age, shallow valleys eroded into the plateau. Nowadays, due to favourable soil conditions, the plateau is largely arable area, but the valleys can be less effectively managed. Valleys preserved semi-natural habitat complexes, consisting of various grassy areas (pastures, hay meadows, unmanaged grasslands), forested patches, wetlands. Each studied grassland patch was part of such smaller or larger semi-natural habitat complex within a valley. The grasslands all fell in the same basic vegetation type of loess steppe, were not currently managed (e.g., not mown, not grazed), but were varied in their properties, such as plant species richness, exposition, etc. The studied grassland patches were always at a peripheral position within the valleys and had a common border with an adjacent arable field. Locality data and basic information about the patches are given in Table 1.

Local and neighbourhood variables. Local botanical characteristics of the grasslands were surveyed at the moth sampling locations, i.e., in the interior and at the edge (see section “Moth sampling”) (Table 2). We included two relief variables for each location: slope and the degree of southern exposition. To avoid the inclusion of a single circular variable among non-circular ones, to express southern exposition, exposition values (originally in degrees) were cosine transformed (Jammalamadaka and SenGupta 2001). Since all grassland patches were situated as part of an incised loess valley, the vegetation based humidity status of the valley bottom, which ranged from being dry to having reed vegetation, was an important neighbourhood variable. We also registered the type of crop adjacent to the patch. Local and neighbourhood variables are listed in Table 2.

Landscape variables. We determined the landscape composition within a circle of 2000 m radius from the middle of each grassland patch based on digitised aerial photographs. The proportion areas of four main habitat types (grasslands, wetlands, wooded areas and arable land) were documented in seven sectors, in circles of the following radii (m): 50, 100, 250, 500, 750, 1000, 2000 (Table 2). In the same sectors, we also documented the proportion area of arable fields taking part in the integrated arable field management AES programme (Hungarian Ministry of Agriculture 2009), placing restrictions on fertilizer and manure output, and making compulsory Integrated Pest Management (IPM) on the fields (according to the Directive 2009/128/EC of the European Parliament). During the selection of the patches, we tried to achieve that they represent as wide a range of the proportion of main habitat types, as it was possible in the given region (Table 1 and 3).

Moth sampling

Sampling design. Moths were collected in 28 locations in the 14 patches listed in Table 1, i.e., in each patch we had two locations. The two locations differed in their position, being either in the interior of the grassland patch or at the edge, neighbouring an arable field. At each location we set up three baited funnel traps hung from a lower branch of a tree or from

Table 1. Locality data of 14 investigated grassland patches. Grasslands were loess steppe patches with various degree of xerophilic character (loess steppe type). Area of the semi-natural complex refers to the part of the valley without cropland. General land use intensity around the patches is indicated by the percentage of semi-natural areas within a 500 m radius landscape sector.

Settlement	Loess steppe type	Latitude (N)	Longitude (E)	Area of semi-natural complex (ha)	Area of grassland patch (ha)	% of semi-natural habitats within R=500 m sector
Székesfehérvár	mesophile	47°14'28.51"	18°26'16.95"	0.5	0.50	2.9
Székesfehérvár	xeromesophile	47°14'40.38"	18°25'41.14"	136.0	0.22	36.4
Aba	xeromesophile	47°6'25.05"	18°32'16.22"	331.0	0.61	37.0
Aba	mesophile	47°6'55.91"	18°31'13.86"	27.1	2.36	10.4
Dég	xeromesophile	46°50'35.37"	18°25'22.98"	50.4	0.27	26.8
Előszállás	xerophile	46°49'18.85"	18°48'24.46"	143.6	1.28	40.2
Igar	mesophile	46°47'17.21"	18°30'19.14"	102.7	0.27	44.0
Igar	mesophile	46°47'18.54"	18°32'2.29"	89.9	0.33	57.5
Mezőszilas	mesophile	46°47'16.00"	18°28'18.47"	35.4	0.38	14.1
Sárbogárd	xeromesophile	46°55'27.13"	18°39'0.12"	5.2	0.20	10.5
Sárbogárd	xeromesophile	46°54'54.89"	18°39'17.01"	64.8	0.36	27.0
Seregélyes	xeromesophile	47°7'40.25"	18°32'36.92"	27.3	0.29	24.9
Vértesacsa	xerophile	47°23'27.55"	18°33'48.88"	144.1	0.53	44.4
Vértesboglár	xerophile	47°24'47.65"	18°31'48.19"	23.9	0.27	22.8

wooden pole at c. 1.5 m height. The three traps were placed in a linear transect, inter-trap distance was 20–30 m. Transects in the two locations were placed at c. 30–80 m distance (as allowed by patch size and shape). Traps were operated during two sampling campaigns: 13. Sept. – 09. Oct. 2011 and 10. Sept. – 08. Oct. 2012. During campaigns, traps were emptied at 4–7 days intervals.

Traps. Funnel traps were the standard CSALOMON® VARL+ funnel traps produced by the Plant Protection Institute, HAS (Budapest, Hungary), which were originally developed for capturing noctuids (Tóth et al. 2000), and proved to be suitable also for some other moths as well (Tóth et al. 2002, Subchev et al. 2004). Photos of the VARL+ trap can be viewed at www.csalomontraps.com. A small piece (1 cm × 1 cm) of household anti-moth strip (Chemotox®, Sara Lee, Temana Intl. Ltd, Slough, UK; active ingredient 15% dichlorvos) was placed in the container to kill the captured insects.

Baits. Iso-amyl alcohol (= 3-methyl-1-butanol), isobutanol (= 2-methyl-1-propanol), and acetic acid were obtained from Sigma-Aldrich Kft. (Budapest, Hungary) and were stated by the suppliers to be >95% pure. For making the baits the 200 µl of the compounds were loaded onto a 1 cm piece of dental roll (Celluron®, Paul Hartmann Ag. Heidenheim, Germany), which was put into a polyethylene bag (ca 1.0 cm × 1.5 cm) made of 0.02 mm linear polyethylene foil. The bait dispensers were heat sealed and attached to 8 cm × 1 cm plastic stripes for easy handling when assembling the traps. The bait compounds dissolve in polyethylene which results in their slow release from the sealed dispensers. Each funnel trap was giv-

en three of such baits as earlier experience showed that triple baits perform optimally (Tóth et al. 2010). In the field, baits were changed once in the middle of the sampling campaigns, as previous experience with similar baits showed that they may start to loose activity after 2–3 weeks time (Tóth et al. 2002).

Data and statistical analysis

Data preparation

Since locations were fairly homogeneous in their vegetation and inter-trap distances were rather low (especially relative to the mobility of Lepidoptera), furthermore catches at individual trap emptying occasions were changeable, we pooled data of all yearly catches within a location and treated it as the basic unit for further analyses (N = 28 per year). By contrast, we treated the interior and margin locations within a patch separately. We considered the small size of the patches, plus that traps at the margin were not much further from traps in the grassland interior than within location trap distances. Still, we chose the separate treatment, because local vegetation at the margin was markedly different from that in the interior, and the distinction gave us the option to test for the effect of small scale environmental variation.

Moths were identified by Cs. Szabóky, who also provided a trait-based classification for each species. The list of moth species caught and their trait classification with class definitions is given in Supplementary Table 1. To describe

Table 2. Complete list of explanatory variables and covariates describing the environment in and around the 14 investigated grassland patches at the three main scales of the study: at local, neighbourhood and landscape scale. Covariates describing spatiality and temporality are also listed here.

Scale, aspect	Variable	Abbreviation	Description	Number of levels/type
local	vegetation richness*	VegRic	plant species richness	8
local	naturalness*		naturalness of vegetation	5
local	weediness*		cover by weed species	7
local	disturbance*		intensity of disturbance, e.g., mowing	3
local	physiognomy	Physgn	degree of stratification of the vegetation	4
local	vegetation height	VegHgh	mean height of vegetation (cm)	cont.
local	shrub dominance	Shrub	dominance of shrubs	7
local	slope	Slope	slope in degrees	cont.
local	southern	South	degree of southern exposition, given as cosine compass degree	cont.
neighb.	crop	NBcrop	crop in neighbouring field (classified as: maize, cereal, dicot)	3
neighb.	neighbourhood richness	NBRic	plant species richness of non-focal part (edge, if interior is focal or vice versa)	8
neighb.	bottom humidity	HumBott	humidity of valley bottom	8
landscape	arable	Arabl	proportion of arable habitat within each of the landscape sectors of the following radii (m): 50, 100, 250, 500, 750, 1000, 2000.	cont.
landscape	meadow	Meadw	proportion of meadow habitat within each of the landscape sectors of the following radii (m): 50, 100, 250, 500, 750, 1000, 2000.	cont.
landscape	wetland	Wetl	proportion of wetland habitat within each of the landscape sectors of the following radii (m): 50, 100, 250, 500, 750, 1000, 2000.	cont.
landscape	wooded	Wood	proportion of wooded habitat within each of the landscape sectors of the following radii (m): 50, 100, 250, 500, 750, 1000, 2000.	cont.
landscape	AES arable	AES_Arabl	proportion of arable habitat in integrated management within each of the landscape sectors of the following radii (m): 500, 1000, 2000.	cont.
spatial	x	x	longitude co-ordinates value in Hungarian Unified Co-ordinate System (EOV)**	cont.
spatial	y	y	latitude co-ordinates value in Hungarian Unified Co-ordinate System (EOV)**	cont.
temporal	Year	Year	year of the study	2

* These variables showed strong intercorrelation, out of them only vegetation richness was used in any analyses. Abbreviations: neighb.=neighbourhood, cont.= continuous.

** EOV is a x,y coordinate system, units in metres

MMA at locations, separately for the two years, we used number of species (SpecNumb), total number of individuals caught (TotCatch), and mean of species traits weighted by the number of individuals caught, as follows (with abbreviation and number of classification levels in brackets): pest status (wPest, 3), polyphagy (wPolyph, 3), number of generations, voltinism (wVoltin, 2), mobility, tendency to migrate (wMobil, 2), body size (wSize, 3). In the case of the species trait 'rarity' (Rare, 4), simple arithmetic mean was used to avoid underweighting rarity and overweighting commonness. We regarded that these parameters describe several aspects of the MMAs, and we used them to describe changes in MMAs in a multivariate way.

Statistical analysis

Multivariate analyses were conducted in Canoco version 5 (ter Braak and Smilauer 2012). We used standard procedures recommended by ter Braak and Smilauer (2012) and

Leps and Smilauer (2003). To explore data structure, Principal Component Analysis (PCA) was applied. Gradient length was determined by Detrended Correspondence Analysis (DCA). Based on gradient lengths, we used Redundancy Analysis (RDA) as a constrained analysis to study the effect of environmental variables. If effects (such as, for instance, year) were needed to be partialled out, we used partial analyses with the effect as covariate. A Monte Carlo permutation test based on 999 random permutations was conducted to test the significance of the eigenvalues of the canonical axes and the marginal and conditional significance of explanatory variables; for the latter Canoco 5 reported pseudo-F test statistics. To avoid over-parametrization of models, we tried to reduce the number of explanatory variables to a meaningful small number, for which forward selection procedures were applied (ter Braak and Smilauer 2012). Canoco safeguards against inflated Type I error estimate when interpreting results in a stepwise selection, by reporting adjusted P values that limits false discovery rate to a specified threshold (0.05) (Smilauer and Leps 2014). Selection was stopped when the adjusted P

Table 3. Proportion of basic habitat types in the landscape in selected sectors around the 14 investigated grassland patches. Landscape sectors are indicated by their radii of circle from the middle point of the patch.

habitat	50 m			500 m			2000 m		
	Mean	S.D.	range	Mean	S.D.	range	Mean	S.D.	range
arable	0.24	0.18	0-0.74	0.71	0.16	0.42-0.97	0.81	0.09	0.65-0.92
meadow	0.69	0.20	0.26-1	0.17	0.11	0.02-0.42	0.06	0.06	0-0.25
wetland	-	-	-	0.01	0.01	0-0.04	0.02	0.02	0-0.07
wooded	0.06	0.10	0-0.36	0.11	0.08	0-0.29	0.05	0.04	0.01-0.17
AES arable	-	-	-	0.13	0.25	0-0.70	0.12	0.13	0-0.36

value reported for the contribution of the next best variable exceeded 0.05.

We wanted to know the conditional effect of local, neighbourhood and landscape variables, the latter in increasing sectors around the grassland patch. For this we used variation partitioning analyses in Canoco 5, which is based on partial RDAs. **Beginning with effects at local scale, the explanatory variables were divided in two groups, i.e., a group of variables describing the focal scale – in this case the local scale (6 variables, Table 2), and a group of variables describing all the other “non-focal” scales, including – in this case – variables of the neighbourhood (3 variables, Table 2) and variables of the surrounding landscape (proportions of main habitat types in each considered sector, 28 variables, Table 2).** Variables Year and those representing spatiality were in all cases included in the non-focal group. We proceeded then the same way for each other effect according to Table 2, always comparing variables of the focal effect to variables of the non-focal effects. When the focal effect was the proportion of habitat types in a given landscape sector (i.e., radii from 50 to 2000 m), the proportions of habitat types in landscape sectors with other radii were not considered in the non-focal effect. For each effect, both groups of focal and non-focal variables were separately submitted to a forward selection of variables and simple effect variation partitioning was performed. Then, in a second analysis we used the selected group variables to establish the conditional effect of the groups (Smilauer and Leps 2014). Supplementary Table 2 shows for each focal effect the explanatory variables in both focal and non-focal groups remaining after forward selection.

To establish the significance of interaction between local and landscape scale effects, we first created one compound variable for both of these scales. This was done by running forward selection partial RDAs (year as covariate) for local and landscape scale variables. Here we applied localness in a broader sense (see the effect “local, sensu lato” in Supplementary Table 2), and let the process select from both “local” and “neighbourhood” variables. Similarly landscape scale was treated more broadly by considering all radii for the variable selection. From the resulting two partial RDA results, we used first axis case scores as representing local and landscape effects as single variables. Finally, a third partial RDA contained the extracted local and landscape first axes scores and their interaction as explanatory variables, plus year as covariate, in order to assess the amount of variation covered by the interaction term.

Results

Sampling MMAs in 28 locations of 14 grassland patches during the 2011-2012 sampling campaigns resulted in a total catch of 30966 individuals belonging to 101 Lepidoptera species in eight families (Supplementary Table 1). Majority of the species (83) and over 97% of the individuals belonged to the Noctuidae family, and only Nymphalidae (6 species) and Pyralidae (5 species) were represented by more than just 1-2 individuals (Supplementary Table 1). Thus, all forthcoming results treat this Noctuidae biased sub-assemblage of Lepidoptera that is accessible by our baited trap method.

A preliminary DCA indicated short gradient length ($SD=0.7$), therefore linear methods were chosen for succeeding analyses. An explorative unconstrained ordination (PCA) showed that year had a strong effect in separating assemblages by their trait parameters. Conducting a subsequent constrained analysis (RDA) with year as the only constraining variable gave the result that this constrained axis was responsible for 17% of the total variation (pseudo- $F=11.1$, $P=0.001$). The inclusion of variables describing spatiality (x , x^2 , y , y^2 , xy) had a weaker effect. A forward selection procedure in partial RDA indicated that x -coordinates had significant effect (pseudo- $F=3.6$, $P=0.014$) and y -coordinates had marginally significant effect (pseudo- $F=1.8$, $P=0.1$), together being responsible for 9.4% of the total variation. Therefore, in all following analyses year and spatiality were included as covariates or were made available in forward selection to be selected. We had vegetation and relief data separately for grassland edges and interiors, and these showed considerable variation. We tested whether position of the location (edge vs. interior) within grassland patch per se had an effect after partialling out year and spatiality. Position had no significant effect (partial RDA: pseudo- $F=1.0$, $P=0.44$), therefore we decided to locally describe each trapping location by the corresponding local (vegetation and relief) parameters and disregard position status.

To examine the basic relationship between MMAs and all environmental variables, we ran a partial RDA (year and spatiality were covariates), including local, neighbourhood and landscape variables as explanatory variables. These accounted for 50.4% of variation, with 31.7% cumulative variation explained by the first two ordination axes (Fig. 1). This ordination indicates that wooded areas had a strong influence, being associated with total Lepidoptera catch and negatively with traits such as pest status, polyphagy, higher generation

numbers and mobility. These correlated, pest status-related variables were in positive association with the amount of arable habitats at 50 and 250 m distances and with the neighbouring crop being maize. Variables describing local and neighbourhood vegetation characteristics (amount of shrubs, physiognomy, species richness in neighbouring vegetation and the humidity of valley bottom) were associated with the mean rarity and the number of species.

As a next step, we made a variation partitioning analysis to see the contribution of explanatory variable groups in explaining MMA characteristics. The unique contribution of the variables describing various focal scales (conditional on vari-

ables in the other non-focal scales) was minimal at the local scale and included shrub cover and vegetation physiognomy. Variables describing habitats in the immediate neighbourhood had moderate, marginally significant effect, including the identity of neighbouring crop and the humidity of valley bottom (Supplementary Table 2). Landscape composition as close as 50 m to the trapping locations had the strongest and highly significant effect on MMAs, being responsible for nearly 10% of total variation (Table 4, Fig. 2). Landscape composition effect in a 100 m circle was somewhat less pronounced, but in a 250 m circle (Fig. 3) was nearly as strong as at 50 m. From 250 m onwards the effect of landscape compo-

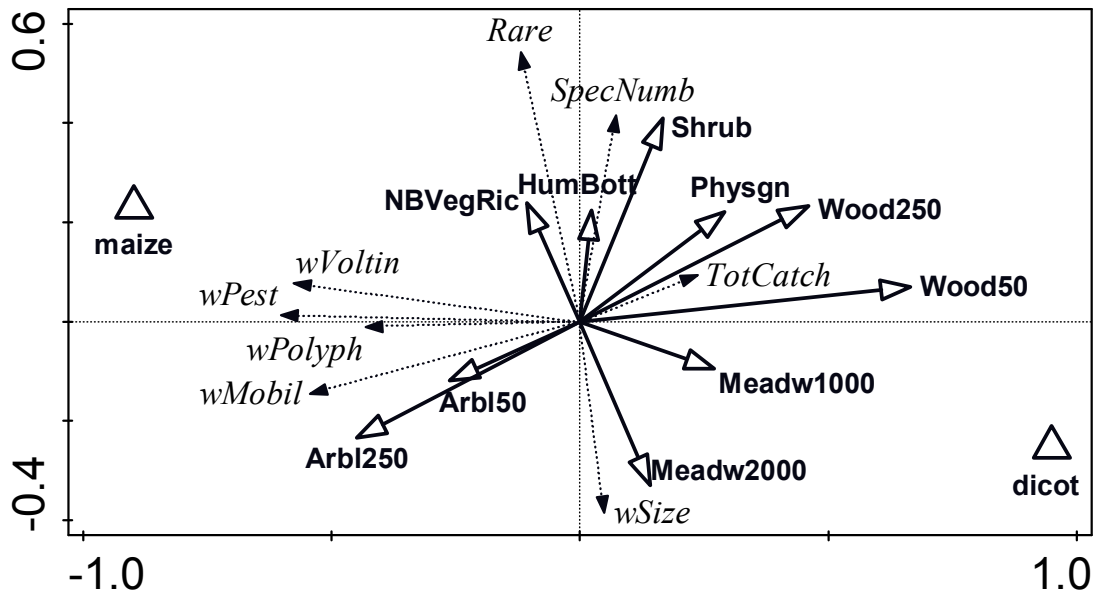


Figure 1. Partial RDA of macro-moth assemblages described by trait-based parameters on local, neighbourhood habitat and landscape level variables. For variable abbreviations, see Table 2.

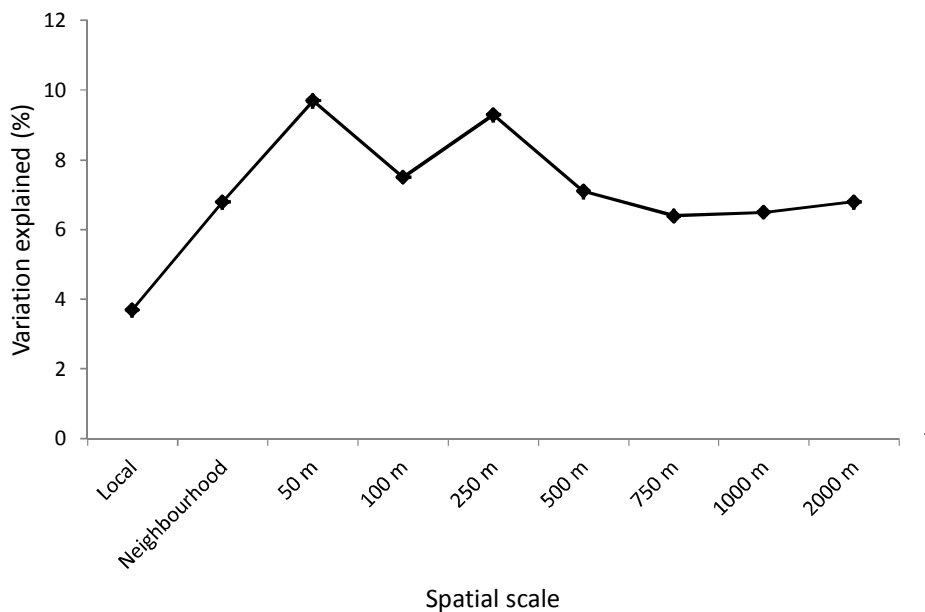


Figure 2. Conditional contribution of variables at different scales to the total variation explained, after accounting for variables describing other scales.

Table 4. Result of variation partitioning analyses based on partial RDAs, separately for each considered scale. The focal fraction (for the given scale) is “a”, group of variables describing non-focal scales are in group “b”. Variables of both groups were forward selected, the group membership for the variables is given in Supplementary Table 2. “c” represents joint effect of groups “a” and “b”.

Scale	Fraction	Variation	% of Explained	% of All	DF	Mean Square	F	P
Local	a	0.033	7.7	3.3	2	0.016	1.3	0.220
	b	0.341	79.9	34.1	7	0.049	3.9	0.001
	c	0.053	12.4	5.3	--	--		
	Total Explained	0.430	100	43	9	0.048	3.8	0.001
	All Variation	1	--	100	55	--		
Neighbourhood	a	0.068	16.5	6.8	3	0.023	1.8	0.041
	b	0.284	69.4	28.4	4	0.071	5.8	0.001
	c	0.057	14	5.7	--	--		
	Total Explained	0.408	100	40.8	7	0.058	4.7	0.001
	All Variation	1	--	100	55	--		
50 m	a	0.097	20.6	9.7	3	0.032	2.8	0.001
	b	0.356	75.6	35.6	7	0.051	4.3	0.001
	c	0.018	3.9	1.8	--	--		
	Total Explained	0.472	100	47.2	10	0.047	4	0.001
	All Variation	1	--	100	55	--		
100 m	a	0.075	16.7	7.5	3	0.025	2	0.022
	b	0.360	80	36	7	0.051	4.2	0.001
	c	0.015	3.3	1.5	--	--		
	Total Explained	0.450	100	45	10	0.045	3.7	0.001
	All Variation	1	--	100	55	--		
250 m	a	0.093	19.9	9.3	4	0.023	1.9	0.015
	b	0.321	68.6	32.1	7	0.046	3.8	0.001
	c	0.054	11.5	5.4	--	--		
	Total Explained	0.468	100	46.8	11	0.043	3.5	0.001
	All Variation	1	--	100	55	--		
500 m	a	0.071	16	7.1	4	0.018	1.4	0.117
	b	0.306	68.6	30.6	7	0.044	3.5	0.001
	c	0.069	15.4	6.9	--	--		
	Total Explained	0.446	100	44.6	11	0.041	3.2	0.001
	All Variation	1	--	100	55	--		
750 m	a	0.064	14.6	6.4	4	0.016	1.3	0.226
	b	0.319	72.7	31.9	7	0.046	3.6	0.001
	c	0.056	12.8	5.6	--	--		
	Total Explained	0.438	100	43.8	11	0.040	3.1	0.001
	All Variation	1	--	100	55	--		
1000 m	a	0.065	14.7	6.5	4	0.016	1.3	0.212
	b	0.367	83.6	36.7	7	0.052	4.1	0.001
	c	0.008	1.8	0.8	--	--		
	Total Explained	0.439	100	43.9	11	0.040	3.1	0.001
	All Variation	1	--	100	55	--		
2000 m	a	0.068	15.3	6.8	4	0.017	1.3	0.173
	b	0.357	80.7	35.7	7	0.051	4	0.001
	c	0.018	4	1.8	--	--		
	Total Explained	0.442	100	44.2	11	0.040	3.2	0.001
	All Variation	1	--	100	55	--		

sition in the landscape was gradually decreasing and was not significant at 500 m and further (Table 4).

We were interested in to what extent and how AES fields in the landscape influence the Lepidoptera assemblages. Like for spatial scales, here we also conducted first a simple ef-

fect variation partitioning analysis between two groups with forward selection. In the focal group we included the proportion of AES fields at 500, 1000 and 2000 m, and the other group contained forward selected variables from other spatial scales (see Supplementary Table 2). The whole model explained 61.7% of total variance (test on 4 calculated axes:

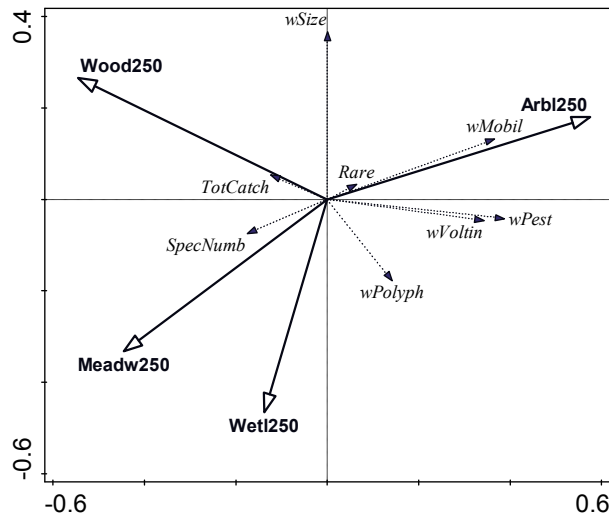


Figure 3. The effect of landscape composition within a circle of 250 m radius. Partial RDA, with covariates controlling for other aspects of the data chosen after a forward variable selection: year, spatiality (x^2 , y^2), local habitat (Shrub, Physgn) and neighbourhood (NBCrop). For variable abbreviations, see Table 2.

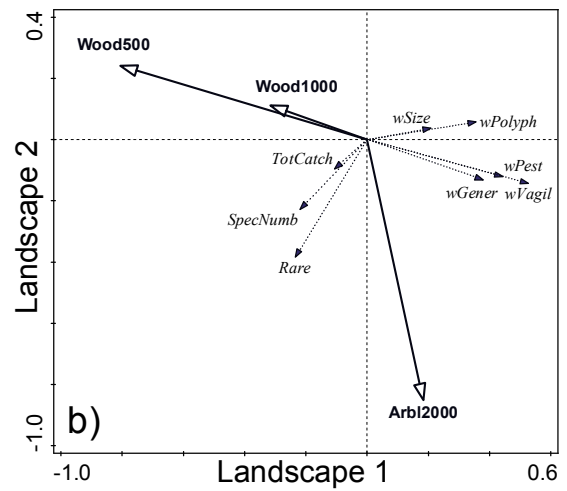
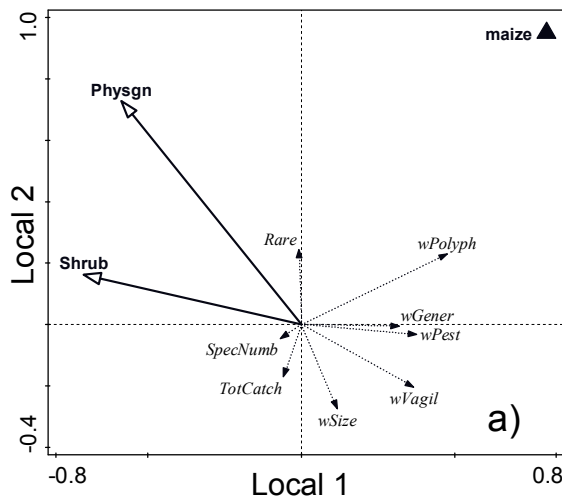
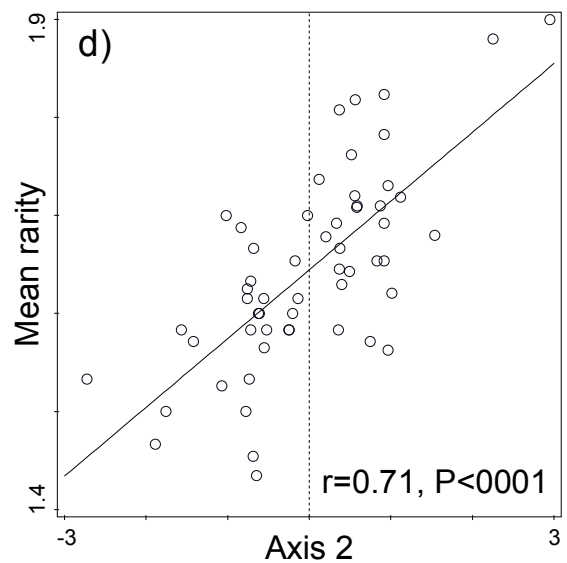
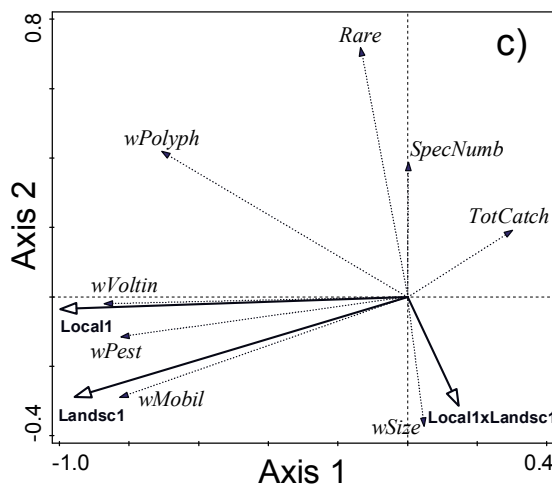


Figure 4. The effect of **a)** local scale (sensu lato) and **b)** landscape scale (sectors of all radii considered) effects on MMA traits depicted on RDA ordination diagrams. In a third RDA (c) the first axes of local and landscape scale RDAs and their interaction were considered. **d)** Relationship of Mean rarity to axis 2 of the interaction RDA, being representative for local \times landscape interaction. Variable abbreviations are in Table 2, details of variables included in the RDA analyses are given in Supplementary Table 2.



pseudo-F=9.5, P=0.001), but, when effects at other scales were partialled out, the unique contribution of AES management in the landscape was only 1.2% of the total variance (2% of explained variance), not significant (pseudo-F=0.5, P=0.73). The AES effects at the three scales were highly correlated with each other and were positively correlated to the total catch of moths and negatively to mobility, pest status and size.

Finally, we wanted to test if there is any interaction between the local quality of the grassland patches and landscape composition in influencing the MMAs. After forward selection (see Supplementary Table 2), in the case of local variables (*sensu lato*) the first axis of the RDA accounted for 11.1% of the total variation (pseudo-F=6.2, P=0.001), being negatively correlated with the local explanatory variables physiognomy and shrub dominance (Fig. 4a). In the case of landscape scale (all radii considered for selection) the first RDA axis accounted for 13.7% (pseudo-F=8.1, P=0.011) of the variation, and was negatively correlated with the cover of wooded areas in the 500 and 1000 m sectors. The amount of arable land within the 2000 m sector had an influence along axis 2 (Fig. 4b). A third partial RDA contained the extracted local and landscape first axes and their interaction, plus year as covariate. This RDA explained 60.9% of the total variation, and the interaction term alone explained 5.3% of variation (pseudo-F=2.9, P=0.035). Interaction effect was especially negatively strong on mean rarity (Fig. 4c). There was a strong relationship ($r = 0.71$, $N = 28$, $P < 0.0001$) between rarity and Axis 2, which had a strong negative relationship with the interaction, as depicted in Fig. 4d.

Discussion

In our study, we asked whether local or landscape scale factors were responsible for shaping the Lepidoptera assemblages of remnant grassland patches in a predominantly agricultural landscape. The detailed multivariate analysis of trait-based assemblage parameters revealed that both scales have important influence, and these influences act on different traits in the assemblages. This trait-based approach is relevant, because it links better the studied assemblages to ecosystem functioning and services (Quetier et al. 2007). A range of environmental variables is likely to act differently on such different traits as, for instance, pest status or rarity. For this reason, we have chosen a multivariate treatment of the different traits which were, where it was meaningful, weighted by species abundance. As Gagic et al. (2015) demonstrated for several animal groups, the integration of the abundance and distribution of not only species, but also of their trait levels is needed for a better understanding of biodiversity and functional relationships in terrestrial animal communities.

We used traps with a special three-component bait that attracted moth species from eight families. The attractiveness of the traps was clearly selective taxonomically, collecting largely noctuid moths, so all results have to be interpreted for the attracted subset of the moth assemblage. This is a common problem of virtually all insect trapping methods, they are based on either intercepting or luring individuals, includ-

ing light traps, but the bias can be acceptable in comparative situations if the interpretation is done for the correct subset of the assemblage (Southwood and Henderson 2000, Merckx and Slade 2014). For studies, where scale dependent habitat characteristics are considered, the effective distance of a trapping method, from which insects are attracted, is of importance. To the best of our knowledge the range of attraction (as defined by Wall and Perry 1987) has not been measured for the feeding attractant used in this study (blend of isoamyl alcohol plus acetic acid). Data available on pheromones (which are generally thought to be much more active than feeding attractants) suggest that our lures could not evoke orientation responses from moths at more than a couple of metres distance. For example, range of attraction of synthetic pheromone was found to be less, than 1 m in the diamondback moth (*Plutella xylostella* L., Lepidoptera, Plutellidae) (Ishii et al. 1981), within 4-5 m (one tree canopy) in *Acrobasis nuxvorella* Neunzig (Lepidoptera, Pyralidae) (Harris et al. 1997), less than 10 m in the western corn rootworm (*Diabrotica virgifera virgifera* LeConte, Coleoptera, Chrysomelidae) (Tóth et al. 2003), and at the most some dozens of m in *Grapholita molesta* Busck (Lepidoptera, Tortricidae). Under tropical circumstances, Uehara-Prado et al. (2007), similarly to the present study, placed their fruit baited traps at ca. 20 m inter-trap distances, studying fruit-feeding butterfly assemblages inside forests. The traps were located at 50 m from forest edge and did not catch species representative of open or edge habitats, indicating that the range of attraction must fall below this distance even in the case of good flyer, large bodied lepidopterans. Thus, we estimate that our sampling method must have trapped moths from the close vicinity of individual traps, and moths were there because of the biotic and abiotic suitability of the environment, and not because the traps had lured them there from greater distances.

In fragmented landscapes, the quality of habitat patches plays an important role in determining species distribution and in regulating spatial dynamics (Mortelliti et al. 2010). Our analysis found a limited role of local variables in determining Lepidoptera assemblages. However, there was a clear tendency that certain assemblage characteristics, such as rarity and species number were more associated to local and neighbourhood variables than to variables describing higher scales. Out of the local variables, shrub cover and physiognomy were important, both related to the structural properties of the vegetation. Somewhat surprisingly, plant species richness of the local vegetation did not influence the MMAs. Similarly to our results, other studies in various settings also found that macro-moth community structure and diversity were related to structural descriptors of the vegetation, but not related to floristic diversity (Axmacher et al. 2009, Highland et al. 2013). Shrubs in particular might be important contributors to vegetation structure, by further diversifying the structural properties of plant communities and contributing to milder temperature regimes in otherwise open areas (Wagner et al. 2003). Shrubs can also provide food resources for larvae of many moths. These structural characteristics had a positive relationship to diversity-related MMA characteristics, such as rarity and species richness, while other characteristics that

may actually make moths less dependent on local vegetation, such as body size and vagility, had a negative relationship to these vegetation variables.

Considering the unique contributions of scales, local vegetation characteristics and relief played a relatively minor role influencing MMAs. While it is the local vegetation that provides resources and microhabitat, the mobility of Lepidoptera may decrease the detectable role of local scale variables. In studies, where compared habitat patches varied little, a similarly limited influence of the local scale and high influence of the landscape scale was found (Grand and Mello 2004, Liivamagi et al. 2014). **However, in studies where local habitat patches encompassed a wider range of habitats** (Collinge et al. 2003, Highland et al. 2013) or habitat management schemes (Pöyry et al. 2009, Facey et al. 2014, Kormann et al. 2015), the importance of local factors was higher.

In the present system, characteristics of the neighbourhood habitats (neighbouring crop type, humidity of valley bottom) and landscape composition at the 50 m scale had higher unique explanatory power, than local habitat characteristics. We interpret the 50 m scale as a habitat area and local habitat diversity effect. In Table 1 areas of the grassland patches are listed (nearly all of them were below 1 ha), but this grassland characteristic was not included in the multivariate analyses. That is mostly because we regarded that there was a high uncertainty in the delineation of individual grassland patches (including those in which the studies were made). This was due to the patchy distribution of various habitat types. While we could designate each pixel on a habitat map to a habitat type, we could not tell which continuous set of such pixels comprises one “patch”. Therefore, it was easier to use overall habitat areas at all scales, including the 50 and 100 m radii, which we regarded as a proxy for patch size. Habitat patch size was found to be an important factor affecting Lepidoptera assemblages in a number of studies (Öckinger et al. 2012, Robinson et al. 2014).

Landscape composition in the landscape at 250 m had the highest influence on the MMAs. The range at which landscape variables have the highest influence must vary with the mobility and resource use pattern of the animal group. Different groups of macrolepidoptera vary in their mobility (Betzholtz and Franzen 2011), but quite unequivocally the highest influence in many studies appeared to be in the range of 250-500 m (Krauss et al. 2003, Fuentes-Montemayor et al. 2011, Liivamagi et al. 2014). The arable field component was associated with species traits such as pest status, migratory capacity, generation numbers and host plant generalist status. At the same time, in our study, the number of moth species caught was in negative relationship with field cover, i.e., in positive relationship with the combination of non-field habitats. Similar relationship between increasing field cover and the same traits was found in a Finnish study in intensively cultivated landscapes, but in that study at lower (<60%) field coverage the relationship no longer held (Ekroos et al. 2010). In the present study field cover (in 2 km radius circle) ranged between 65-92%, thus, at any rate, the areas counted as intensively cultivated landscapes. Our findings, and those in Ekroos et al. (2010), indicate that even in such generally

intensively managed landscapes different levels of intensity matter, and can alter assemblage traits to better or worse. The proportion of AES fields among the arable fields also represents management intensity, but in the present system, even though their presence had a considerable variation (0-36% coverage in 2 km radius), their unique contribution was not significant. This raises the question whether basic AES programmes are themselves significantly different from normal management, but the present study was not designed to test this.

If local and landscape scale effects are studied, the question of interaction between them also arises. We found a significant interaction between local and landscape level effects, which explained a modest variation. Interestingly, rarity showed the strongest association to the interaction, indicating that both local and landscape scale factors are important in the preservation of this valuable MMA characteristic. While both local and landscape scale effects are of a compound nature, considering the main local and landscape level factors which have the strongest association with the respective compound effects (such as depicted on Fig. 4) can help the interpretation. “Local 1” axis described a negative effect of shrub dominance and physiognomy, while “Landscape 1” axis had a negative relationship with the main explanatory variable woodland cover in more than one landscape sector. Their interaction pointed the opposite direction of rarity and species number. This can be interpreted, as contrasting situations having a positive effect on rarity (and species number), i.e., when wooded areas are missing in the landscape, then shrub cover and more complex local physiognomy favours rarity, but the opposite scenario may also hold, when local vegetation is structurally less diverse, then woodlands in the landscape will increase rarity level in MMAs. The average size of the moth species reacted the opposite way, structurally more homogeneous landscape and local conditions favoured larger (and more common) species. Nevertheless, we have to keep in mind that the interaction explained a relatively low amount of variance. Relatively short gradients in landscape scale variables were likely to limit interaction effects. We find this case in studies with similarly short landscape scale gradients, such as in Kormann et al. (2015), whereas interaction effects in studies with longer gradients were more pronounced (Rundlöf and Smith 2006, Ekroos et al. 2010, Ekroos and Kuussaari 2012). In spite of the interactions, the present study highlights the contributions of both local and landscape scales to the shaping of MMAs and suggests that the preservation of both local habitat quality and landscape heterogeneity are important if we would like to maintain a species rich and functionally diverse Lepidoptera fauna.

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Table 1. List of all macro-moth species caught during the study, with the total number of specimens caught, and their designated trait values.

Table 2. Included variables in groups a and b after forward selection in simple effect two group variable partitioning analysis.

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