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ORIGINAL PAPER

Grassland butterfly communities of the Western Siberian forest steppe in the light of post-Soviet land abandonment

Johanna Trappe[1] · Friederike Kunz[1] · Sarah Weking[1] · Johannes Kamp[1]

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Abstract Land-use change and homogenization of the landscape are severe threats to butterfly diversity. The break-up of the Soviet Union in 1991 led to land abandonment on very large scales. This study aims at assessing the impact of the ongoing abandonment of traditionally managed grasslands and subsequent vegetation succession on butterflies in Western Siberia, a species-rich area with butterfly communities similar to those of Central and Eastern European grasslands. 20 mown and 20 abandoned grasslands were surveyed using Distance Sampling methods in summer 2015. We recorded 997 individuals from 44 species, pooled over two sampling events. An indicator species analysis and detrended correspondence analysis revealed that communities likely underwent changes in species composition during succession, and that habitat specialization decreased. In contrast to previous studies we found no evidence of early stages of abandonment being more species-rich than mown meadows. On unmanaged grasslands litter cover and litter depth were significantly higher than on mown grasslands. Half of the abandoned sites were riparian meadows. The dynamics and ecological characteristics of the floodplain had a stronger influence on community composition than land use. This study shows that structural heterogeneity and lepidopteran diversity of the vast, but understudied, Western Siberian grasslands are driven by mechanic and natural disturbance. Conservation should aim at responding to trends of abandonment and actively maintaining a mosaic with grasslands of different successional stages.

Keywords Land-use change · Secondary succession · Distance sampling · Conservation · Floodplain

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✉ Johanna Trappe
Johanna.trappe@wwu.de

[1] Biodiversity and Ecosystem Research Group, Institute of Landscape Ecology, University of Münster, Heisenbergstr. 2, 48149 Münster, Germany

Introduction

Accelerating extinction rates as a consequence and symptom of global change are causing growing concern as loss of biological diversity significantly deteriorates the efficiency of both ecosystem functions and services (Cardinale et al. 2012; Pimm et al. 1995). Land-use change is considered the most important threat to terrestrial biodiversity (Sala 2000) and encompasses the intensification of as well as the abandonment of agriculture (Henle et al. 2008; Queiroz et al. 2014; Settele et al. 2009). While production has increased on high-yielding and accessible sites, traditional land-use systems, such as extensive livestock grazing and haymaking, as well as associated semi-natural grassland habitats have declined drastically during past decades (Rey Benayas 2007; MacDonald et al. 2000).

The Palearctic grasslands are considered biodiversity hotspots and especially important for invertebrates (Dengler et al. 2014). For more than half of Europe's Lepidoptera species grasslands are the main habitat (van Swaay et al. 2006, 2015; Habel et al. 2013). Regardless of habitat type, European butterfly populations have substantially declined across vast areas during the past decades. Intensification and land abandonment are consistently mentioned as major drivers of butterfly declines (Habel et al. 2016; van Swaay et al. 2006). Grassland specialists are especially affected (van Swaay et al. 2006, 2015), whereas mobile species with a wide habitat breadth favoring eutrophic biotopes are thought to be less vulnerable (Kuussaari et al. 2007; Nilsson et al. 2008). This may lead to community impoverishments with a shift from many specialized species to few generalists (Habel et al. 2016). However, negative trends for generalist species like *Pieris rapae, Thymelicus lineola, Gonepteryx rhamni* and *Aglais urticae* have also been reported (van Dyck et al. 2009), stressing the critical state of butterflies in Europe overall.

In the Russian Federation, vast areas (about 1/4 of the landmass) are covered by grasslands including tundra, zonal steppes, azonal and extrazonal grasslands such as floodplains, and semi-natural grasslands maintained by man (Dengler et al. 2014; Schepaschenko et al. 2011). After the break-up of the Soviet Union in 1991, agriculture in Russia transitioned from a state-controlled to a market oriented system. Times of economic hardship, the withdraw of subsidies and fast privatization during the 1990s led to the abandonment of 2.6 million ha of cropland across Russia (Prishchepov et al. 2013; Wesche et al. 2016), of which only a very small proportion has been recultivated since. Livestock numbers collapsed in the same period, with a decline of 70% in cattle numbers (Wesche et al. 2016). This was caused by a decrease in large-scale meat and dairy production, but also by a strong trend of rural outmigration and associated declines of livestock kept by villagers for subsistence. Livestock declines led to abandonment of hay meadows and pastures, the area of which remains unquantified, but probably even exceeds the figure for abandoned cropland.

In contrast to Western and Central Europe (where abandonment effects on invertebrates are comparatively well established) there are few assessments of the consequences of rapid land management changes after the end of the Cold War era on biodiversity (Sutcliffe et al. 2015). Across the former Soviet Union, most studies have addressed vegetation restoration after abandonment (Brinkert et al. 2016), or changes in mammal (Bragina et al. 2015; Sieber et al. 2015) and bird (Herzon et al. 2014; Kamp et al. 2011) communities and populations. Studies on invertebrates are largely lacking.

We studied the effect of abandoning grasslands formerly used for hay cutting on butterfly communities in Western Siberia. We selected this region as butterfly communities are still rich in comparison with most Central European grasslands, and as the area is a hotspot of grassland abandonment in Russia.

When trying to quantify anthropogenic disturbance and successional age vegetation height is commonly considered an easily measurable indicator that increases subsequent to abandonment (Pöyry et al. 2006; Stefanescu et al. 2009). According to the structural diversity hypothesis tall grassland vegetation has a higher structural diversity and therefore provides many suitable niches for grassland butterflies (Collinge et al. 2003; Öckinger et al. 2006; Pöyry et al. 2006).

Insect herbivores are known to show weak disturbance tolerance compared to plants and most findings claim butterfly diversity to be negatively associated with disturbance (Huston 1994). Contrastingly, plant diversity peaks at intermediate levels of continuous disturbance and thus at lower vegetation (Connell 1978). Butterfly species richness is positively correlated with floral diversity and availability of nectar flowers and host-plants (Bergman et al. 2008; Cremene et al. 2005; Curtis et al. 2015). Therefore, unfertilized mown or lightly grazed sites can also be an attractive habitat (Erhardt 1985; Kati et al. 2012).

The trade-off between little disturbance and high floristic diversity results in a unimodal response of butterfly diversity to vegetation height with an overall shift towards higher vegetation (dynamic equilibrium model) (Pöyry et al. 2006). In terms of Lepidopteran species richness few previous studies have shown a decline or no change after the onset of succession (Öckinger et al. 2006; Steffan-Dewenter and Tscharntke 1997; Dolek and Geyer 1997). Most often highest richness was found in recently abandoned grasslands diversely structured with a mix of herbs, tall grasses and low shrub cover (Balmer and Erhardt 2000; Cremene et al. 2005; Erhardt 1985; Kati et al. 2012; Pöyry et al. 2004; Skórka et al. 2007; Söderström et al. 2001).

Based on these findings we anticipated that

(1) differences in diversity and species composition of butterfly communities can be found on mown and abandoned grasslands in Western Siberia,
(2) the habitat structure of grasslands in succession can be linked to the abundance of butterfly indicator species, and
(3) a mosaic of extensively managed meadows and grasslands in early successional stages following land abandonment therefore increases total butterfly diversity in the Western Siberian landscape.

The aim of this study is to evaluate the ecological integrity of the present butterfly communities compared to European grasslands and to derive recommendations for butterfly conservation in a poorly studied part of the world.

Materials and methods

Study region

The West Siberian Plain stretches from the Ural Mountains in the West eastwards to the Yenisei River (Suslov 1961; Zakh et al. 2010). Our study area encompasses 20 by 20 km and is located in the southwestern part of the Lowland northeast of the city of Tyumen (Tyumen province) and near the village Kaskara. Biogeographically it is placed in the hemiboreal forests ecoregion (Fig. 1).

Elevation in the study area varies between 50 and 70 m a.s.l. and water availability, pedogenesis and vegetation are determined by differences in meso- and micro-relief (Kämpf et al. 2016).

Leached chernozems, phaeozems and podsolized grey forest soils can be found in elevated and well-drained areas, where cropland alternates with park-like deciduous forests. These subtaiga birch stands (*Betula pendula*) subdominated by *Populus tremula* mark the transition between the boreal zone to the north and the forest steppes to the south (Olson et al. 2001; Schmithüsen 1976; Walter and Breckle 1994) and are considered the easternmost extensions of the temperate deciduous forests found in Europe (Nimis et al. 1994). Gleysols, Fluvisols and Histosols are common soils in the vast floodplain of the Tura river and in drainless sinks filled with lakes, peatlands and wet grasslands in near-natural state or used as extensive meadows and pastures (IIASA and RAS 2002; Selezneva 1973). Along the river terraces or on relict sand dunes coniferous *Pinus sylvestris* forests grow on podzolic Regosols (Selezneva 1973). Fires are a frequent disturbance in the area (Tchebakova et al. 2009).

The climate is continental with an average temperature of 2.3 °C and annual precipitation of 482 mm at Tyumen weather station (Menne et al. 2016). Winters are cold and relatively dry with a monthly average of −15.0 °C in January, while summers are hot. During the sampling period 2015 June was extraordinarily warm and wet, while July was very cool and typically wet (Menne et al. 2016). The vegetation period is 160 days (Selezneva 1973).

Sampling design

As we were interested in the effect of a cessation of mowing on butterflies, we selected 20 plots on used (GMO) and 20 on abandoned hay meadows (GAB). Due to the limited accessibility in the terrain, plot locations were not chosen randomly but placed in several clusters with transects being at least 1000 m apart. Random sampling was not feasible because of logistic constraints. Half of the GAB sites (n = 10) were located on floodplain grassland. Availability of GMO plots was restricted in the Tura floodplain. We

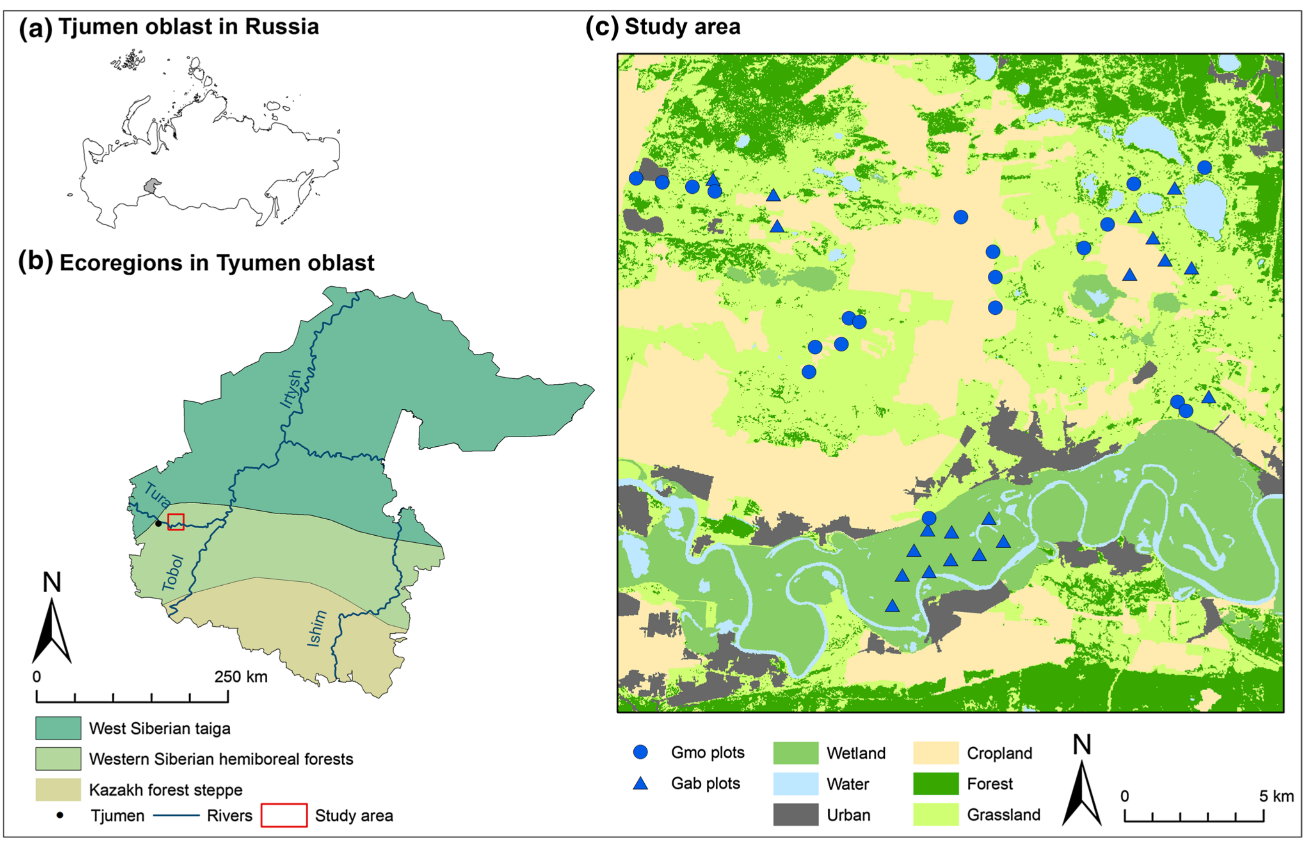

Fig. 1 Location of Tyumen oblast (grey) in Russia (**a**) and the study area's location in Western Siberian hemiboreal forests as one of three ecoregions present in Tyumen oblast (**b**) and sampling plots as well as land cover within the study area (**c**) (Chen et al. 2015, http://www.globallandcover.com; GADM 2015; Natural Earth 2016; Olson et al. 2001; Mathar et al. 2015)

acknowledge that these issues may result in spatial autocorrelation, but consider these limitations minor as the study area is characterized by small-scale heterogeneity.

Abandonment was determined using high resolution satellite images and aerial pictures available in Google Earth before fieldwork started. Fourteen images from the period 2003 to 2015 were available. Fields were characterized as GMO when evidence of mowing during the previous 3 years was visible (mowing tracks, haystacks). Hayfields were classified as GAB when traces of mowing were last visible on images older than 3 years (most had been abandoned much earlier). At each plot, evidence of mowing (usually visible for at least the preceding 2 years) was recorded during fieldwork, and the remote sensing-based classification corrected where discrepancies were obvious. Abandoned croplands were excluded from sampling. Their location was determined based on an available classification of satellite images (cf. Weking 2016).

Butterfly surveys

The sample plots were surveyed twice between June 1st and August 2nd, 2015. All butterfly species (incl. Hesperidae) were counted along standardized Pollard Walks of 200 m length (Pollard 1977). To be able to correct for varying detection probabilities across species, butterfly observations were assigned to distance categories (Isaac et al. 2011) and later analyzed using Distance Sampling (Buckland et al. 2008). Distance sampling is a method to obtain more accurate abundance data in the form of population densities, while butterfly diversity remains unaltered. Five distance intervals were used: 0–2.5 m (Pollard Walk box), 2.5–5 m, 5–10 m, 10–20 m and over 20 m perpendicular on either side of the transect line.

Individuals were caught with hand-held nets or identified with the help of binoculars (8 × 42). Morphologically similar species that could not be distinguished reliably in the field were combined to taxon groups (*Pontia edus*a and *Pontia daplidice*, as well as *Melitaea athalia, Melitaea aurelia* and *Melitaea britomartis*). Field research was conducted daily during the 2-months sampling period on condition that weather conditions were favorable. No counts were done when wind speeds exceeded 5 Bft. or temperatures stayed below 13 °C on unclouded days and 17 °C on days with overcast sky (cloud cover < 40%). Due to the short vegetation period in the study area, we assume the flight period of most species was covered. As we were more interested in comparing communities and population densities between land-use types, a full species inventory was beyond our scope.

We also collected data on habitat variables: in the center of each transect line the cover of grass, herbs, bushes and plant litter were estimated in percent within a 5 by 5 m sampling quadrat. Maximum vegetation height and average depth of the litter layer were recorded in centimeters on each of the four corners of the sampling quadrat and averaged. Signs of fire or recent flooding (presence/absence) were also recorded.

Statistical analyses

Distance measurement data were used to calculate effective strip-width (ESW, the distance at which equally many individuals within the transect bounds are overlooked as are seen beyond) by fitting half-normal or hazard detection functions using the model of Royle et al. (2004) in package *unmarked* (Fiske and Chandler 2011) in R version 3.2.3 (R Core Team 2015). Competing models were compared using AIC_C. Population densities (ha^{-1}) for each species-plot combination were estimated using the equation

$$\hat{D} = \frac{n}{a} = \frac{n}{2ESW \times L},$$

where n is the number of individuals observed, L the length of the transect and a the covered area (Buckland et al. 2008). This correction for variation in detection probability was made for all taxa with sufficient sample size (≥ 20 transects). For species with a lower sample size, ESWs of closely related species with similar body size and flight behavior were used (e.g. the ESW of *Argynnis aglaja* was used for *A. adippe*, following Buckland et al. 2008) (refer to Online Resource).

Shannon index and species evenness were calculated for each plot, using data from the visit with the highest density of each species. Measures of species diversity and vegetation structure were tested for significant differences between habitat types by means of Kruskal–Wallis tests with Bonferroni correction of p-values.

Similarity of plots as well as species composition in relation to habitat structure were explored through multivariate analysis of the abundance data, restricted to the standard Pollard box (i.e. excluding detections beyond 2.5 m). Environmental variables were standardized by z-transformation. We performed a detrended correspondence analysis (DCA) with the 'decorana' function (R package *vegan*, Oksanen et al. 2016), excluding species with low frequencies (recorded on <5% of transects) and selecting the survey round with the higher count (either June or July).

An Indicator Species Analysis in PCORD 6 (McCune and Mefford 2011) was used to reveal characteristic species (indicator value IV ≥25) of mown grasslands, abandoned/near-natural flood meadows and other abandoned grasslands. Significance of indicator values was evaluated with a Monte Carlo test with 4999 permutations. Generalized linear models (GLM) were used to evaluate correlations between habitat parameters and species abundance (with negative binomial error distribution), and habitat parameters and diversity measures (with Gaussian or negative binomial error distribution) to identify important drivers of abundance and community patterns. Standardized environmental parameters were also fitted as squared variables to allow for hump-shaped relations. Collinearity problems were avoided by including only one of a pair of correlated (Spearman' s rho <0.7) variables. Model fit was assessed using Akaike's Information Criterion for small sample sizes (AIC_c) and all possible models fitted and compared with function 'dredge' in R package *MuMIn* (Barton 2016). We set a threshold of $\Delta AIC_C \leq 4$ to select the best supported models (Burnham and Anderson 2002). Variable importance $w_+(j)$, a measure of the times a variable is included in the total number of fitted models weighted by their AIC_C, was calculated with function 'importance'. Coefficients were averaged using function 'model.avg' in R package *MuMIn* (Barton 2016).

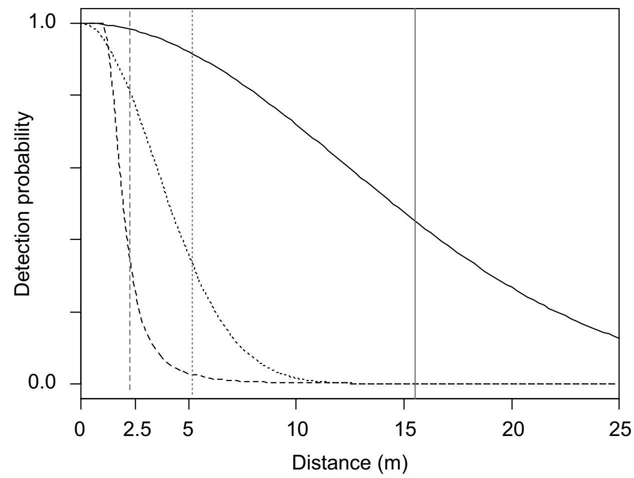

Fig. 2 Comparison of detection probability functions (black curves) and ESW (grey vertical lines) for highly detectable *Pieris rapae*/*P. napi* (solid), intermediate *Aphantopus hyperantus* (dashed) and inconspicuous *Thymelicus lineola* (dotted) at average vegetation height 70 cm

Results

Species-specific detectability

In total, 477 butterflies were observed on mown grasslands and 520 on abandoned hay meadows. 62% of individuals were observed within 2.5 m of the transect line, i.e. the standard Pollard Walk box. Five species were only detected beyond these limits.

Species detectability in the field was heterogeneous. Figure 2 shows the detection probability as a function of distance from the observer for three common and representative taxon groups with varying visual apparency at an average vegetation height of 70 cm. ESWs for all species separately are listed in Online Resource A1.

Across all species mean and median ESW averaged 5.80 and 4.80 m. At a distance (*w*) of 2.5 m from the observer all species could be spotted easily, the average detection probability was 98%.

Habitat structure of mown and abandoned grasslands

Eleven of 20 GAB sites were located in the Tura floodplain and differed in habitat structure compared to other abandoned plots as well as meadows in use (Online Resource A2). While herb densities were similar across all sites, grass tended to grow less dense on floodplain sites compared to GMOs ($p = 0.084$) and other abandoned plots ($p = 0.187$) (Fig. 3). Vegetation height was highest on abandoned plots outside the floodplain and lowest on hay meadows, but differences in mean were insignificant. A Kruskal–Wallis test revealed that abandoned plots were covered with a significantly thicker and expansive litter layer than mown sites. Although litter density was intermediate on abandoned flood meadows and typically some ground was covered by moss, bare soil was exposed significantly more often. Shrubs grew on some of the abandoned plots, but never exceeded a cover of 25%. None of the plots was grazed regularly.

Community diversity

Across all study sites γ-diversity was 44 and α-diversity ranged between 3 and 18 species per plot (mean 8.90 ± 3.79 SD). Mown hay meadows (GMO) were slightly less diverse in total (36 species), but on average more species per plot were found (mean 9.20 ± 4.23 SD) than on abandoned sites (GAB; 38 species, mean 8.60 ± 3.39 SD). In terms of α-diversity (S), Shannon diversity index (H') or evenness (E), no significant differences between land-use types or location within/outside the floodplain were found (Fig. 4).

Community resemblance

A detrended correspondence analysis revealed a large overlap in species composition of some unmanaged grasslands with mown sites (Fig. 5a), while butterfly communities on floodplain meadow plots were distinctive. The first axis of the DCA was positively correlated ($p < 0.05$) with cover of moss, predominantly present on abandoned floodplain grasslands (Spearman's rank correlation, $\rho = 0.6995$, $p < 0.0001$). Accordingly, centroids of sites naturally disturbed by flooding and fire were positively associated, whereas sites mown during the field campaign had negative scores with the axis. The axis length of 4.12 SD-units indicated a complete species turn-over along the gradient and accounted for 13.5% of variation. Species composition changed significantly

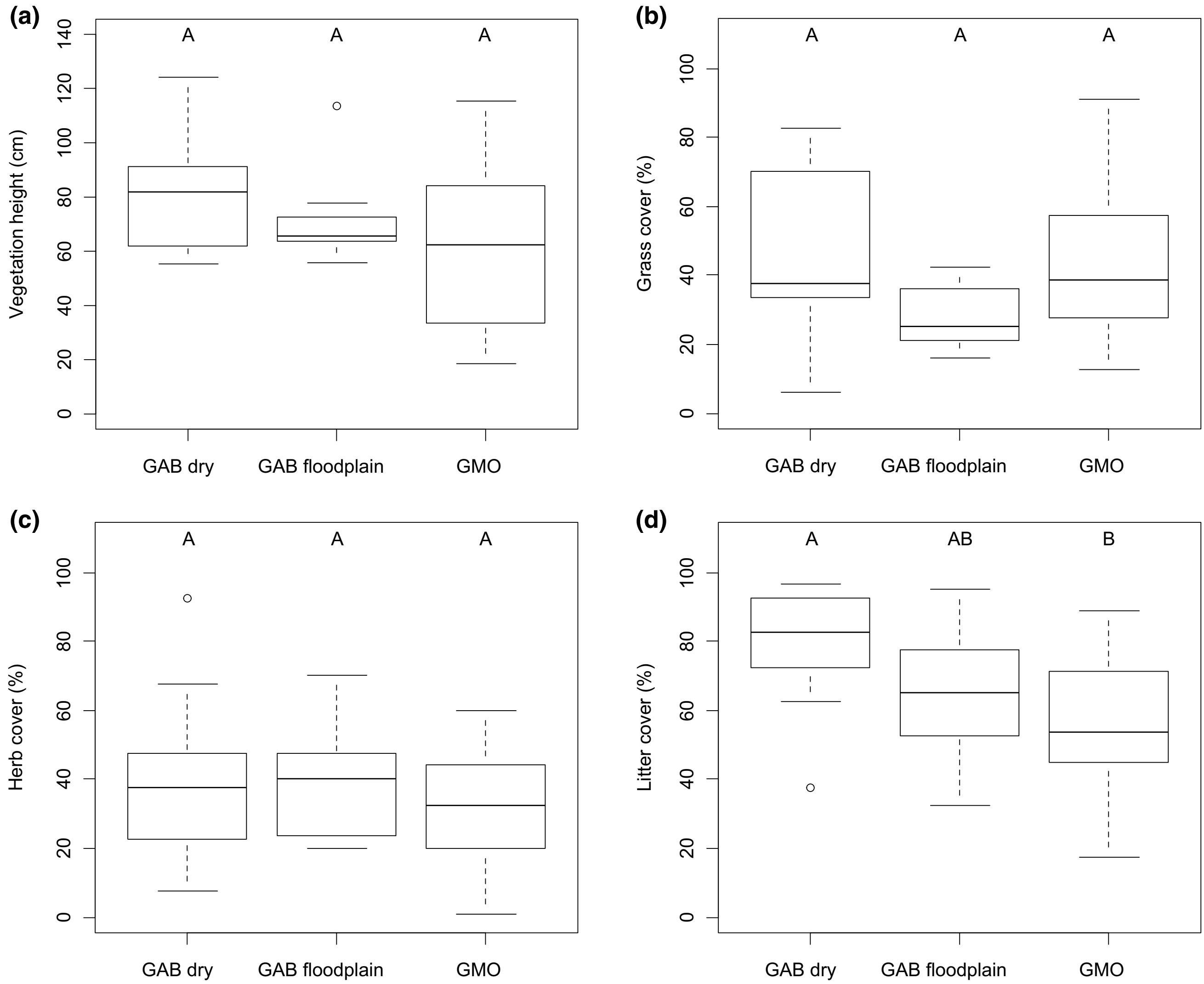

Fig. 3 Habitat parameters of meadows (GMO) and abandoned sites (GAB) located within or outside of floodplain. Different letters in groups indicate significant differences (Kruskal–Wallis test, $p < 0.05$)

along the second axis (3.14 SD-units), that separated grassy sites ($p = 0.001$) from those with a high proportion of bare ground ($p = 0.073$). In total, the ordination explained 21.6% of variation.

Indicator species for the land-use categories and habitat quality

An indicator species analysis (Table 1) revealed grassland butterfly communities typical of mown and abandoned plots (Fig. 6). Findings corresponded with grouping of species in the DCA (Fig. 5b).

Generalized linear models were calculated for floodplain indicators (*Argynnis aglaja, Hyponephele lycaon, Minois dryas, Papilio machaon*), significant indicators of other unmanaged sites (*Aphantopus hyperantus, Pieris rapae, Coenonympha glycerion, Cyaniris semiargus*) and GMO indicators (*Aglais urticae, Pontia daplidice*/*P. edusa, Cupido argiades*). Online Resource A3 gives detailed information on the models. GLMs of *Coenonympha glycerion* and *Pieris rapae* gave no convincing indication of habitat preferences.

GLMs revealed that flood meadow indicator species tended to be more abundant on plots with an intermediate vegetation height (Table 2). They were more likely to occur on sites with sparse vegetation, neither dominated by grass nor herbs, a thin litter layer and plenty of bare ground. Models of three indicators were negatively correlated with the categorical variable land use, suggesting other significant factors typical of (alluvial) GAB sites exist that were not included in the GLMs. High vegetation and intermediate grass cover were predictors for species indicative of GAB sites outside the floodplain.

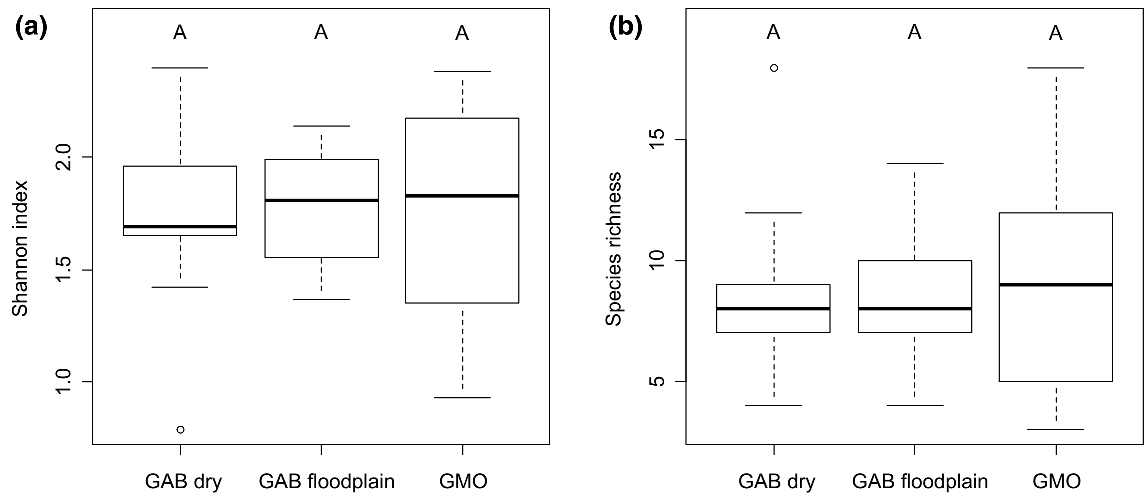

Fig. 4 Shannon diversity index (H') and species richness (S) of butterflies by habitat type based on modelled densities. All differences between habitat types were non-significant (Kruskal–Wallis test, $p<0.05$)

Corresponding with the high variation in site conditions, trends for indicator species of hay meadows were not uniform. Although individuals of *Aglais urticae* and *Cupido argiades* were tolerant of a wide range of vegetation height, sites with tall plants were clearly favored. *Pontia daplidice/P. edusa* only occurred on sites with more than 40% litter cover, whereas a thin (< 5 cm) and relatively low or intermediate cover of litter was predictor for *Cupido argiades* and *Aglais urticae*. Densities of *Pontia daplidice/P. edusa* were highest at low to intermediate herb covers under 40%, but *Aglais urticae* preferred high herb cover. A positive response to land use, thus to habitats influenced by mowing, was evident in the GLMs of *Aglais urticae*.

Discussion

Species detectability

Although general detectability of butterflies on the studied sites was relatively high compared to a study from Europe (Isaac et al. 2011), distance sampling proved to be an effective tool to overcome sampling bias and directly compare species abundances. Inter-species variability in visibility was high and abundance ratios between species differed considerably from results attained through the Pollard Walk: within 250 cm of transect line *Pieris napi* was the second most commonly observed species, but detectability correction suggested that ten inconspicuous and under-recorded species reached higher densities than the Green-veined White.

The importance of habitat-specific and regionally estimated ESWs became obvious when comparing the ESWs calculated by Isaac et al. (2011) and our results. While *Thymelicus lineola* was considered especially noticeable in British habitats it was one of our least detectable species. These findings suggest that variation among open sites is high and pooling data across grassland types to attain a bigger sample size might be misrepresentative. Although it was not assessed how differences in vegetation height, one of the main parameters distinguishing GMOs and GABs, affected detectability, other factors in habitat structure or habitat-specific butterfly behavior may lead to differences in detectability (Isaac et al. 2011; Dennis 2004).

Changes in butterfly diversity and species composition during succession

Despite high inter-site variation, average habitat structure of mown and abandoned grasslands showed strong similarities and supported tall vegetation alike. Low management intensity (e.g. small-scale haymaking relatively late in July) on the one hand and relatively slow succession in the Western Siberian forest steppe (Kämpf et al. 2016) on the other hand may be an explanation for these similarities. In line with Balmer and Erhardt's (2000) findings, hay meadows and early abandoned land varying only slightly in floristic composition showed considerable butterfly community resemblance and were both moderately species-rich. Accordingly, our results showed no significant differences in species number, Shannon index (Fig. 4), evenness or abundance. Similar patterns in orthopteran richness in the study area were observed by Weking et al. (2016).

Despite the prolonged process of habitat differentiation (i.e. relatively slow succession due to the short vegetation period) in Western Siberia, some species indicative of varying disturbance regimes could be identified. Typically, species separate along a disturbance gradient according to life history traits and habitat requirements characterizing

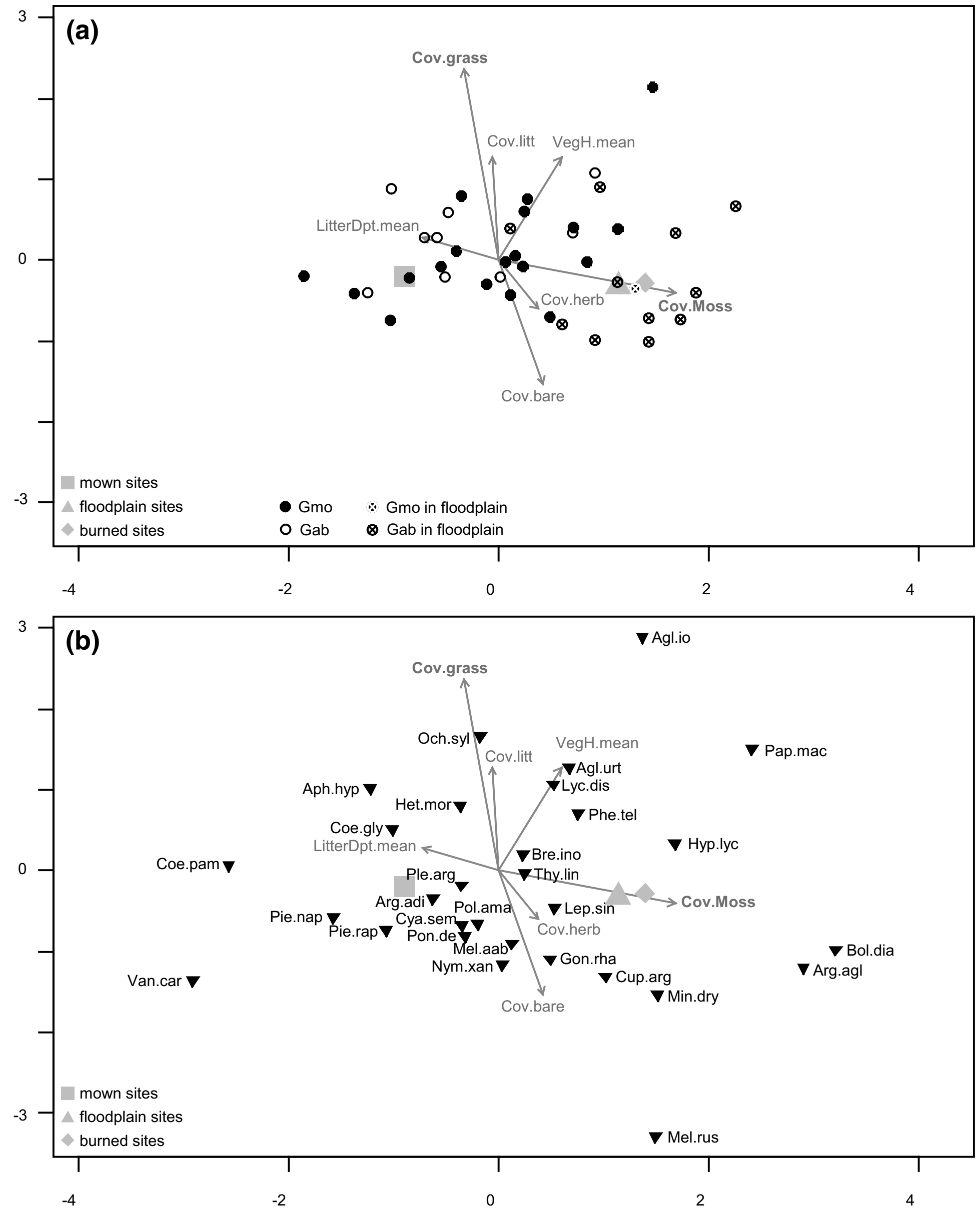

Fig. 5 Ordination (DCA) diagram of the investigated grassland sites (**a**) and butterfly species (**b**) with scores of the first two ordination axes and correlated habitat parameters ($p < 0.05$ in bold). The closer sites or species are arranged to each other in the biplot, the more similar they are. For species codes and environmental parameters see Online Resource A1 and A2

communities of managed or unmanaged grassland. Specialist species with a narrow dietary and habitat niche follow the richness pattern of vascular plants more closely and are more common in mown plots with short vegetation (Pöyry et al. 2006; Wenzel et al. 2006). During later successional stages, when perennial grasses become more abundant, generalists more dependent on sufficient biomass production than on suitable host-plants dominate (Steffan-Dewenter and Tscharntke 1997; Stefanescu et al. 2009).

Regardless of land-use type the majority of indicator species in our study are not considered grassland specialists on a European level (van Swaay et al. 2006, Online Resource A4), but the trend towards generalization associated with proceeding succession could also be observed in our study. All seven GAB indicator species (excluding floodplain indicators) were polyphagous and/or grass-feeders in their larval stage, whereas the GMO indicators were more specialized and reliant on a mix of Fabaceae, Urticaceae and Brassicaceae (Stettmer 2007). The results of the GLM analysis supported these findings: the grass-feeding *Aphantopus hyperantus* (GAB indicator) was more abundant on plots with intermediate grass cover and *Pontia daplidice/P. edusa* typical of managed sites required intermediate herb cover (Table 2). Regardless of land-use type most indicators preferred higher vegetation. For indicators of abandoned grasslands, such as *Cyaniris semiargus*, this may indicate tall grasses as a habitat requirement or—in combination with the explanatory variable “Land.use”—specific high-growing herbal host-plants (*Urtica dioica*) in the case of *Aglais urticae*.

Table 1 Indicator species with indicator value (IV) ≥ 25 referring to habitat highlighted in bold, frequencies (f) and densities (animals/ha) including standard error

Species	IV	p	GAB (riparian)		GAB (other)		GMO	
			f (%)	density ± SE	f (%)	density ± SE	f (%)	density ± SE
Papilio machaon	79.9	***	**91**	**4.36 ± 0.71**	–	–	25	0.60 ± 0.24
Argynnis aglaja	63.6	***	**64**	**3.35 ± 1.16**	–	–	–	–
Minois dryas	62.6	***	**91**	**21.15 ± 5.17**	33	5.97 ± 3.14	45	3.58 ± 1.09
Hyponephele lycaon	52.4	*	**91**	**16.47 ± 3.28**	44	7.55 ± 4.90	60	4.53 ± 0.97
Gonepteryx rhamni	39.0	*	**55**	**1.74 ± 0.56**	22	0.33 ± 0.22	15	0.37 ± 0.24
Melanargia russiae	33.7	*	**36**	**2.39 ± 1.16**	–	–	5	0.19 ± 0.19
Boloria dia	36.4	**	**36**	**2.69 ± 1.29**	–	–	–	–
Aphantopus hyperantus	53.6	**	9	1.32 ± 1.32	**67**	**30.13 ± 11.74**	45	6.05 ± 3.40
Pieris rapae	42.9	*	–	–	**67**	**2.35 ± 0.76**	50	1.31 ± 0.34
Coenonympha glycerion	41.9	*	9	0.69 ± 0.69	**67**	**9.01 ± 4.83**	50	10.37 ± 3.50
Cyaniris semiargus	35.0	**	–	–	**44**	**3.77 ± 1.64**	10	1.02 ± 0.74
Plebejus argus	32.7	0.13	18	1.74 ± 1.16	**44**	**27.67 ± 13.06**	45	8.15 ± 2.63
Heteropterus morpheus	31.0	0.10	18	3.35 ± 2.70	**67**	**9.00 ± 3.20**	25	7.00 ± 3.56
Aglais urticae	33.1	0.37	27	3.03 ± 2.41	67	5.02 ± 2.81	**70**	**6.94 ± 3.84**
Pontia daplidice /P. edusa	28.7	0.12	9	0.91 ± 0.91	22	2.24 ± 1.48	**45**	**5.53 ± 1.54**
Cupido argiades	27.5	0.16	18	4.2 ± 3.34	–	–	**40**	**9.32 ± 5.02**

*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$

A decline of Lycaenidae during succession, due to a lower abundance and variety of Fabaceae, reported by other authors (Stefanescu et al. 2009; Balmer and Erhardt 2000) could not be observed. However, Pöyry et al. (2005) have highlighted that successional preferences of individual species vary in different geographic regions.

The largest number of significant indicator species could be defined for floodplain meadows. This confirms Sabo et al.'s (2005) anticipation that riparian habitats support a distinctly different butterfly community, but are not more species-rich than non-floodplain sites. Naturally occurring disturbance by flooding shapes the vegetative composition and structure, geomorphology, hydrology, microclimate and fire regime of floodplains and consequently leads to dissimilarities in butterfly species composition (Dwire and Kauffman 2003; Fies et al. 2016).

In contrast to tall and relatively dense vegetation, the mosaic of bare ground, compact accumulations of litter, dry moss and open short vegetation creates a heterogeneous microclimate with many warm and dry microhabitats (Eilers et al. 2013; Stoutjesdijk and Barkman 2014). In the riparian zone these favorable microclimatic conditions are a product of frequent flooding and fire and provide an open habitat for (xero)thermophilic species such as *Hyponephele lycaon* and *Cupido argiades*. The equally high abundance of *Cupido argiades* along with *Coenonympha glycerion, Pontia edusa/daplidice* and *Melitaea athalia/M. aurelia/M. britomartis* on mown plots demonstrates that human disturbance and litter removal may also facilitate the presence of thermophilic species.

Although strong declines in both plant and butterfly diversity followed abandonment once succession reached a densely covered forest stage (Balmer and Erhardt 2000), sparsely wooded abandoned/near-natural grasslands can host a large number of plants and butterflies (Cremene et al. 2005; Söderström et al. 2001; Pykälä et al. 2005). Species requiring shrubs or trees (e.g. *Minois dryas, Argynnis aglaja, Gonepteryx rhamni, Aphantopus hyperantus, Coenonympha glycerion*) for foraging resources or shelter enlarged the species pool.

Alluvial meadows featured a low grass cover and rich herbaceous vegetation of intermediate height supplying indicator species with a wide range of host and nectar plants: Violaceae (*Argynnis, Boloria*), Apiaceae (*Papilio machaon*), Fabaceae (*Cupido argiades*), Rosaceae (*Phengaris*), Rhamnaceae (*Gonopetryx rhamni*), and Poaceae (*Minois dryas, Hyponephele lycaon, Melanagria russiae*) (Stettmer 2007).

Land-use change and the importance of Russian grasslands for butterfly conservation

Across the seven provinces of the Western Siberian grain belt (Altay Kray, Chelyabinsk, Kurgan, Novosibirsk, Omsk, Sverdlovsk and Tyumen) 23% of land has remained near-natural or extensively managed secondary grassland (Kühling et al. 2016). The proportion of grassland in our study area is even greater (43.2%) and the land-use intensity is below the average of Tyumen district (Kühling et al. 2016). Three-quarters of grasslands are relatively pristine and have never been ploughed (Mathar et al. 2015). Our study shows that the

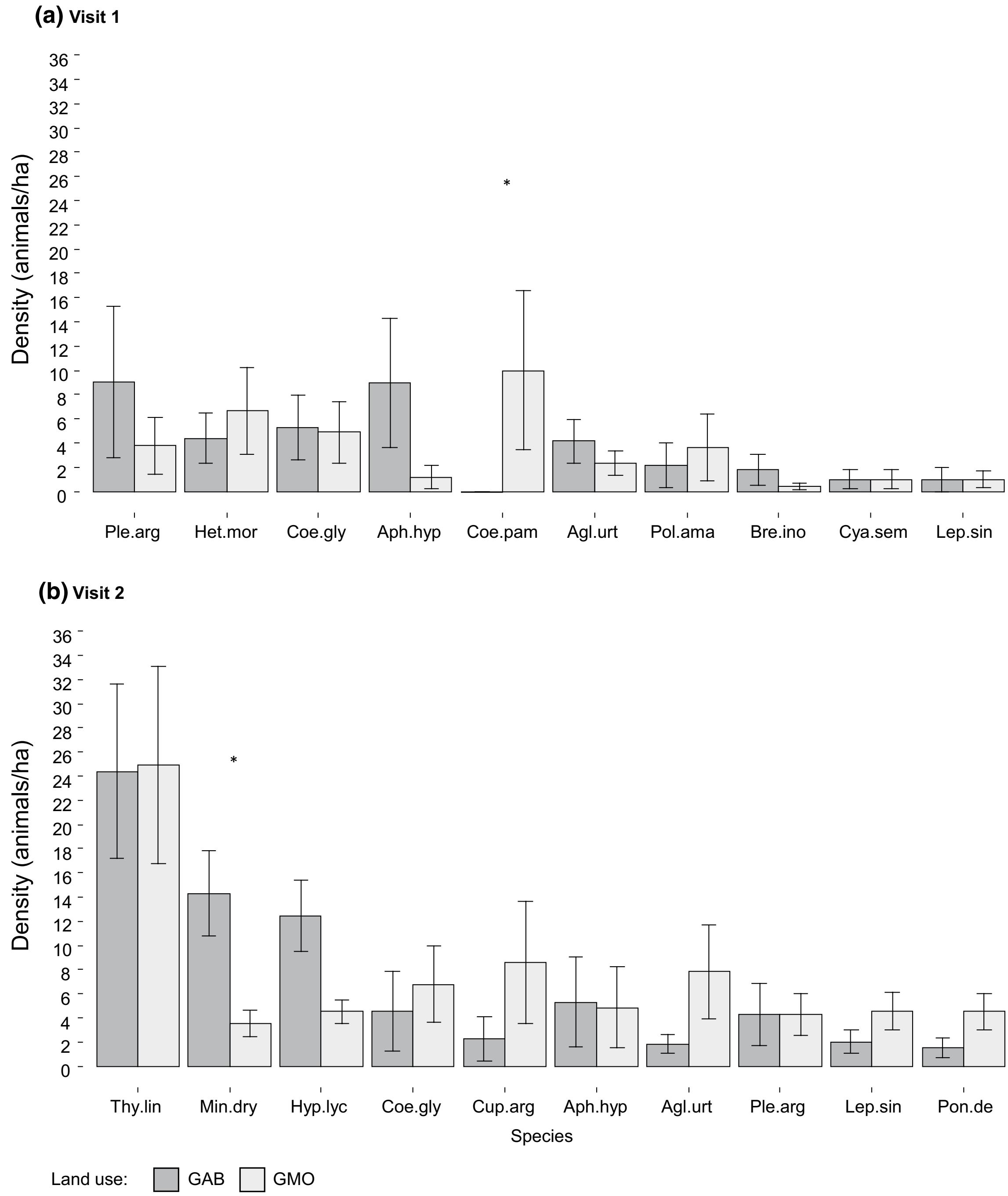

Fig. 6 Mean modelled densities of the ten most abundant species and associated standard errors by land-use type in June (**a**) and July (**b**). For species abbreviations refer to table A1 in supporting online material. *$p<0.05$ (Mann–Whitney U Test)

high structural diversity both within and between sites sustains a high butterfly diversity and is characteristic of these extensively managed hay meadows and abandoned grasslands. Species that are now included in the Red Lists of Germany and/or Europe (Online Resource A1) were common findings in our study. These include *Coenonympha glycerion, Cupido argiades* and *Melitaea athalia*/*M. aurelia*/*M. britomartis* on mown plots. Threatened specialists such as *Phengaris teleius, Phengaris nausithous, Lycaena dispar* and *Lycaena alciphron* occurred on semi-natural grasslands.

In addition to a decrease in total grassland area, threats to open-habitat butterfly biodiversity in Europe as well as Russia include the abandonment and afforestation of less productive areas and an intensification of land use on easily accessible sites (van Swaay et al. 2006; Herrando et al. 2016). The impacts of these contrasting processes

Table 2 Summary of species-specific generalized linear models with ΔAICc <4, including relative importance (Imp) and average estimates and standard error (SE) of explanatory variables. Quadratic variables indcidated by a supercript 2, importances ≥50 highlighted in bold

Species	Imp (%)	Averaged parameter estimate	± SE
GAB (riparian) indicators			
Argynnis aglaja			
Cover of grass	**100**	−2.9228	
Cover of herbs	**100**	−1.4768	
Land.use	**100**	−36.9326	
Hyponephele lycaon			
Vegetation height	**100**	0.1209	± 0.2913
Vegetation height^2	**100**	−0.6470	± 0.1849
Cover of bare ground	**62**	0.4802	± 0.2254
Cover of herbs	19	−0.4655	± 0.2338
Minois dryas			
Land.use	**62**	−1.6759	± 0.7063
LitterDpt.mean	49	−0.5454	± 0.3309
Vegetation height	43	0.2920	± 0.3594
Vegetation height^2	37	−0.6040	± 0.2463
Cover of bare ground	19	−0.0044	± 0.3223
Cover of grass	19	−0.3215	± 0.3223
Papilio machaon			
Vegetation height	**100**	−1.6590	± 0.7818
Vegetation height^2	**100**	−1.8702	± 0.6581
Land.use	35	−1.0272	± 0.5477
Cover of herbs	20	−0.4998	± 0.3275
Cover of moss	16	0.2640	± 0.1978
GAB (other) indicators			
Aphantopus hyperantus			
Cover of grass	**87**	2.7945	± 0.9668
Cover of grass^2	**80**	−1.6348	± 0.5219
Vegetation height	46	0.7095	± 0.4339
Cover of bare ground	32	−1.1930	± 0.7643
Cyaniris semiargus			
Vegetation height	**100**	1.0204	± 0.7031
Litter depth	19	−0.2612	± 0.6823
Cover of grass	19	−0.1865	± 0.7304
GMO indicators			
Aglais urticae			
Vegetation height	**79**	0.7292	± 0.3382
Land.use	45	1.2179	± 0.5515
Cover of bare ground	39	0.5362	± 0.3118
Litter depth	26	−0.4341	± 0.3164
Cover of herbs	18	0.5416	± 0.5145
Cover of grass	16	0.6301	± 0.6065
Cover of litter	15	−0.2546	± 0.2992
Cupido argiades			
Cover of litter	**62**	−2.3056	± 0.9950
LitterDpt.mean	**61**	−2.1644	± 1.2469
Cover of litter^2	38	−1.7105	± 0.6776
Vegetation height	22	0.7160	± 0.6354
Cover of grass	19	−0.7868	± 0.7098
Cover of herbs	14	−0.2269	± 0.6912
Cover of bare ground	13	0.5626	± 0.6743
Pontia daplidice/*P. edusa*			
Cover of herbs	**74**	−1.5682	± 0.7457
Cover of herbs^2	**74**	−1.3276	± 0.6488
Cover of litter	**74**	0.2271	± 0.4487
Cover of bare ground	26	−0.1210	± 0.4624
Land.use	26	1.4036	± 0.9095

The dummy variable land.use could take values of 0 (GAB) and 1 (GMO)

are similar: long-term reduction of nectar and host plant diversity and unfavorable microclimatic conditions. Trends of grassland land-use intensity in the Tyumen area and the entire Western Siberian grain belt have been consistently negative for the past 20 years (Kühling et al. 2016).

In our study, several species typical of different seral stages on grassland were found and both land-use types contributed to the overall diversity of the region. Diversity on extensively mown plots varied with habitat structure: some of the most species-richest and species-poorest sites were managed grasslands. Specialized and threatened species were more frequent and abundant on GMOs than GABs. Nevertheless, the highest number of species was found on an abandoned site with small *Salix* shrubs and a heterogeneous herb cover. Therefore, counteracting long-term abandonment and intensification, and preserving a mosaic of different successional stages would be most beneficial for butterfly diversity. Various experts (van Swaay et al. 2012; Cremene et al. 2005; Bubová et al. 2015) recommend satisfying habitat requirements of single species and entire butterfly communities through spatio-temporal heterogeneity on a landscape scale. Practical implementation includes maintaining and reestablishing active pastoral systems through between-year rotational management of the different seral communities in form of extensive grazing or hay cutting. Temporally varying cutting dates across the area, mowing outside of flight periods to conserve nectar sources and host plants and regionally different grazing intensity (0.2–0.5 livestock unites per ha) would be beneficial conservation measures (Bubová et al. 2015; van Swaay et al. 2012). Simply removing shrubs to counteract long-term succession on abandoned sites is not suitable for maintaining species richness (Hansson and Fogelfors 2000). On the other hand, conserving woodland-grassland ecotones should be a further priority in grassland management.

As these measures require both coordination and financial support, designating target areas for grassland conservation, as Kühling et al. (2016) suggest, would be appropriate. Due to the vast, diverse and relatively pristine grasslands and low cropland intensity found the study area and its surroundings this could be an appropriate starting point. Bringing back livestock to abandoned grasslands could further enhance heterogeneity and the area's suitability for the protection of butterflies and other grassland species.

Moreover, the near-natural riparian meadows of the Tura river intersecting the study area are of high conservation concern. River systems in the northern hemisphere are strongly affected by water regulation, fragmentation and floodplain degradation (Dynesius and Nilsson 1994) and floodplains have become globally endangered habitats (Tockner and Stanford 2002). The butterfly community found on the alluvial meadows was distinctly different from adjacent grasslands and included highly abundant specialists threatened in Germany and Europe (*Hyponephele lycaon, Minois dryas, Argynnis aglaja, Boloria selene, Euphydryas maturna, Lycaena virgaureae*). Preserving and improving the fluvial dynamics and fire regime should be the main priority to avoid sudden shifts of ecological characteristics and species composition (Larsen and Alp 2015). Extensive grazing of riparian systems should only be implemented after careful consideration (Middleton 2013).

We conclude that the study area supports rich lepidopteran communities of different successional stages that can serve as umbrella species for animal groups highly dependent on man-made and natural grassland biotopes. With respect to globally declining biodiversity and trends of abandonment and intensification monitoring and active steps towards conservation are necessary to maintain these communities.

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