



Conservation of a strongly declining butterfly species depends on traditionally managed grasslands

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Abstract

Introduction: Due to land-use intensification at productive soils and abandonment of marginal farmland, biodiversity has dramatically declined throughout Europe. The dryad (*Minois dryas*) is a grassland butterfly that has strongly suffered from land-use change across Central Europe.

Aims/Methods: Here, we analysed the habitat preferences of adult *M. dryas* and the oviposition-site preferences in common pastures located in mire ecosystems of the German pre-Alps.

Results: Our study revealed that plot occupancy was equal at common pastures and control plots. However, the abundance of *M. dryas* was higher at common pastures, although the composition of vegetation types did not differ between the two plot types.

Discussion: Open fens and transition mires traditionally managed as common pastures or litter meadows (= meadows mown in autumn to obtain bedding for livestock) were the main habitats of *M. dryas* in our study area. They offered (i) sufficient host plants (*Carex* spp.), (ii) had a high availability of nectar resources and (iii) a vegetation that was neither too sparse nor too short. In contrast, both abandonment and intensive land use had negative impacts on the occurrence of the endangered butterfly species.

Implications for Insect Conservation Based on our study and other recent research from the common pastures, we recommend to maintain the current grazing regime to foster biodiversity in general and *M. dryas* in particular. Additionally, where possible, abandoned fens and transition mires adjacent to common pastures should be integrated into the low-intensity pasture systems. The preservation of traditionally managed litter meadows is the second important possibility to conserve *M. dryas* populations.

Keywords Grazing · Habitat structure · Host plant · Land-use change · Mire ecosystem · Mowing

Introduction

During the past 200 years, humankind has altered the environmental conditions on earth at an unparalleled rate (Rockström et al. 2009), causing a dramatic loss of biodiversity (Sala et al. 2000; Foley et al. 2005; Barnosky et al. 2011; Cardoso et al. 2020). For terrestrial biomes, land-use change is considered the major driver of the current biodiversity

crisis (Sala et al. 2000; Foley et al. 2005). However, climate change is increasingly becoming an important threat (IPBES 2019). Concerning insects, since the beginning of the industrial era, at least 250,000 species are estimated to have become extinct (Cardoso et al. 2020) and another 500,000 species are assumed to face extinction (IPBES 2019).

Europe is a continent dominated by agriculture (Eurostat 2018). Within farmlands, land-use intensity drives biodiversity. Agricultural ecosystems managed by low-intensity farming practices are of especially high relevance for biodiversity conservation (Veen et al. 2009; Halada et al. 2011). However, due to land-use intensification at productive soils and abandonment of marginal land (Foley et al. 2005; Henle et al. 2008; Kleijn et al. 2009), farmland biodiversity has dramatically declined throughout Europe (Stoate et al. 2001; Krause et al. 2011). As a result, the majority of farmland

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species, such as plants, insects or birds, are highly threatened (Marshall et al. 2003; Donald et al. 2006; Flohre et al. 2011; Storkey et al. 2012).

Butterflies have (i) a pronounced host-plant specificity (Munguira et al. 2009), (ii) narrow niches of the immature stages (García-Barros and Fartmann 2009) and (iii) usually form metapopulations depending on a network of suitable habitats in close proximity (Anthes et al. 2003; Eichel and Fartmann 2008; Stuhldreher and Fartmann 2014). As a result of such complex requirements, butterflies have



Fig. 1 Habitat of *Minois dryas* in a common pasture in the Bavarian pre-Alps

experienced stronger declines than many other taxonomic groups (Thomas et al. 2004; Thomas 2005) and are a major model group in ecology and biodiversity conservation (Watt and Boggs 2003; Ehrlich and Hanski 2004).

The dryad (*Minois dryas*) is a grassland butterfly of Euro-Siberian distribution that has strongly declined throughout Central Europe (van Swaay and Warren 1999; Reinhardt and Bolz 2011; Kalarus et al. 2013; Sachtleben and Winterholler 2013; Kalarus and Nowicki 2017). Due to these declines and our poor knowledge on the habitat requirements, Beneš et al. (2002) called for detailed research on the ecology of *M. dryas* to derive suitable conservation measures. Recently, two studies from Poland and one study from Japan have been published on the habitat selection of adult *M. dryas*. In contrast, for the German pre-Alps, one of the most important strongholds of the species in Central Europe (Sachtleben and Winterholler 2013; Hermann 2020), comparable studies are missing so far. Environmental conditions in the pre-Alps strongly differ from those of the study areas in the aforementioned research; for example, *M. dryas* habitats at the northern foothills of the Alps are mainly located in different types of mire ecosystems (Sachtleben and Winterholler 2013). Additionally, oviposition-site preferences have never been investigated in detail.

In this study, we analyse (i) the habitat preferences of adult *M. dryas* and (ii) the oviposition-site preferences of the species in common pastures located in mire ecosystems

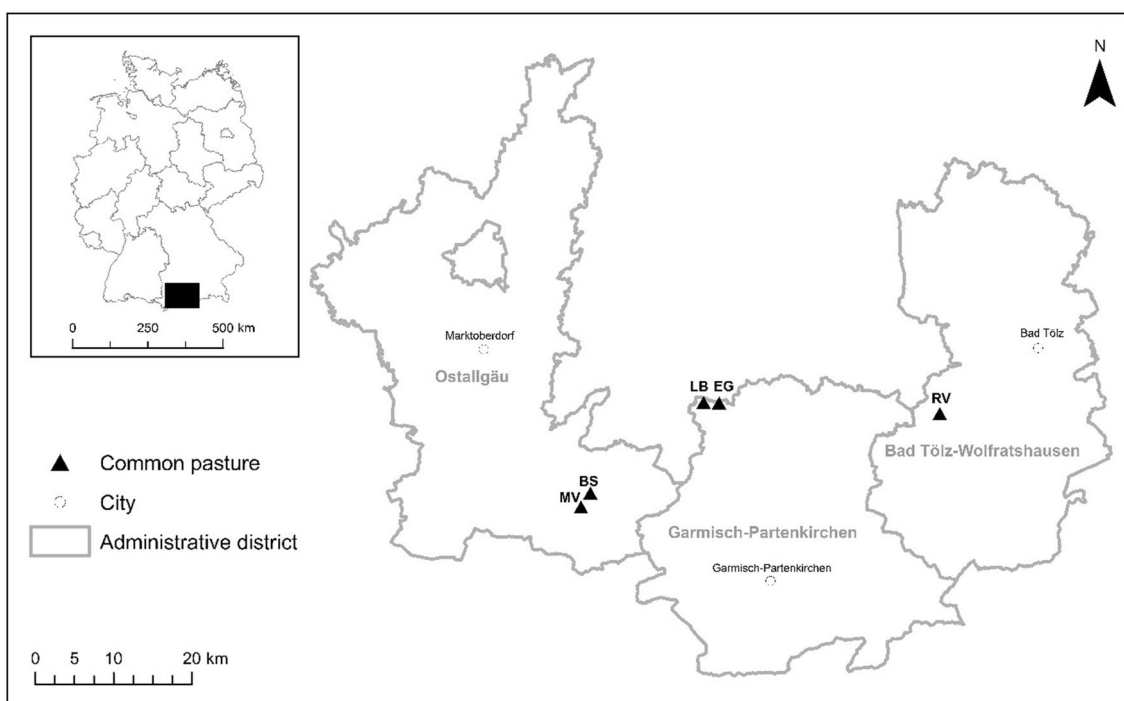


Fig. 2 Location of the study area and common pastures in Upper Bavaria (Southern Germany). Common pasture: *BS* Berghofer Söldner, *EG* Echelsbach Gschwend, *LG* Lettigenbichl, *MV* Mühlenberger Viehweide, *RV* Rieder Viehweide

of the German pre-Alps. Common pastures are traditional, low-intensity grazing systems where different farmers of a village community, the commoners, graze their livestock. The study area is one of the last regions in Central Europe, where large common pastures of high conservation value have remained (Figs. 1 and 2) (Lederbogen et al. 2004; Helbing et al. 2014; Schwarz et al. 2018). However, the effects of grazing on *M. dryas* populations in mires have so far been subject to controversial discussions. According to observations of Sachteleben and Winterholler (2013), the species is able to tolerate low-intensity grazing. However, in a study by Dolek et al. (1994), densities of *M. dryas* were higher in litter meadows (= meadows mown in autumn to obtain bedding for livestock) than in pastures. Based on the results of our study, we discuss the relevance of common pastures for the conservation of *M. dryas* in Central European landscapes.

Materials and methods

Study area

The study was conducted in southern Bavaria (Germany) in the northern foothills of the Alps (550–850 m a.s.l.) (Fig. 2). The study area (hereafter referred to as the pre-Alps) is characterised by a rather cool and wet climate (mean annual temperature: 7.7 °C, mean annual precipitation: 1336 mm; meteorological station Bad Kohlgrub [742 m a.s.l.]; period: 1992–2019; German Meteorological Service 2020). In the heterogeneous young moraine landscape, a small-scaled mosaic of different land-use types has developed, with grasslands used for dairy farming as the most common one (BfN 2012). Within the glacially formed hollows and valleys, mires have evolved (Succow and Jeschke 1990). Due to the relief heterogeneity and the continued traditional way of life of the local people, the land-use type characteristics for old cultural landscapes have remained. For habitats such as common pastures and litter meadows, the pre-Alps are the most important stronghold in Central Europe (Anthes et al. 2003; Lederbogen et al. 2004; Streitberger et al. 2012; Weking et al. 2013; Schwarz et al. 2018). Common pastures are usually grazed by brown dairy cows with a low stocking capacity of 0.5–2.0 livestock units per hectare from May to October (Lederbogen et al. 2004). Besides large areas of grasslands on mineral soil, the common pastures consisted especially of groups of trees, forests, fens, transition mires (= mires that are transitional in ecological characteristics between fens and raised bogs) and raised bogs (= ombrotrophic mires with a surface above the surrounding terrain) (Schwarz et al. 2018). Common pastures have largely not been fertilised, except grasslands on mineral soils (Lederbogen et al. 2004).

Study species

The dryad (*M. dryas*) is a species of Euro-Siberian distribution with a range extending from northwest Spain, France, Central Europe, the Alps, northern Italy, the Balkans and southern Russia to Japan (Sachteleben and Winterholler 2013). In Europe, *M. dryas* inhabits both dry and wet nutrient-poor grasslands (Kalarus et al. 2013; Sachteleben and Winterholler 2013; Kalarus and Nowicki 2017). In Germany, the northern foothills of the Alps are the most important stronghold of the species (Sachteleben and Winterholler 2013; Hermann et al. 2020). Here, *M. dryas* especially inhabits litter meadows or different types of mires (Sachteleben and Winterholler 2013). Adults are on the wing from July to September. Females oviposit their eggs during flight or when shortly sitting on exposed grasses (Ebert and Rennwald 1991; own observation). Caterpillars feed on different species of Poaceae and sedges (*Carex* spp.) (Ebert and Rennwald 1991; Sachteleben and Winterholler 2013; Hermann 2020). Plants with red, pink, violet or blue flowers, such as *Eupatorium cannabinum* or *Succisa pratensis* are preferred as nectar sources (Weidemann 1995; Sachteleben and Winterholler 2013). Due to large-scale habitat loss (Hermann 2020), *M. dryas* is considered endangered in Germany (Reinhardt and Bolz 2011).

Experimental design

Field sampling was conducted during the main period of adult activity (see Sect. 2.2) from July to August 2015 on five randomly selected common pastures and their adjacent grasslands and mires (hereafter referred to as subareas) in the pre-Alps (Fig. 2). Within these five subareas, we randomly selected 55 plots with a size of 500 m² (20 m × 25 m) in common pastures. To compare data from the common pastures with those of the surrounding grasslands on mineral soil and open mires, 55 control plots having the same size were randomly chosen in these habitats in a distance of 20 m to the fence of the respective common pasture.

Adult habitat

All 110 plots were visited twice during suitable weather conditions (warm [> 18 °C] and sunny days without precipitation and strong wind) using standardised transect walks (Pollard and Yates 1993; Streitberger et al. 2012; Weking et al. 2013). All *M. dryas* individuals were counted walking stripe-like and slowly for 15 min through the plots (Krämer et al. 2012; Fartmann et al. 2013). The vegetation type of the plots was assessed using character plant species according to Oberdorfer (1992) and Dierßen and Dierßen (2008). Additionally, vegetation height was measured at three random points and averaged for further analysis. Vegetation density

was determined at 10–15 cm and 25–30 cm height from the ground (Poniatowski and Fartmann 2008). The cover of shrubs, Poaceae, sedges (*Carex* spp.), rushes (*Juncus* spp.), herbs, mosses, open soil and litter was estimated visually in 5% steps. In common pastures, the density of droppings was ascertained at a randomly selected subplot of 100 m² by counting the number of cow pats and horse droppings as a proxy for grazing intensity. The potential sunshine duration during the flight period in August was measured with a horizonscope after Tonne (1954). Additionally, in all control plots, the land-use type (fallow, mown once, mown twice or more often) was recorded.

We quantified nectar abundance after each transect walk by counting all inflorescences in a subplot of 12 m² (3 m × 4 m) (Krämer et al. 2012; Fartmann et al. 2013). We moved the subplot to where most of the flowers within the plot were found during the transect walk to take the mobility of *M. dryas* into account. We weighted nectar abundance according to its use by the butterfly derived both from literature data (Ebert and Rennwald 1991) and our own field observations. Flowers that were visited frequently received a higher preference class (*PC*) than unpopular ones (Krämer et al. 2012). To calculate the weighted nectar abundance (NA_i) of the nectar plant species *i*, we used the following formula (Fartmann et al. 2013):

$$NA_i = na_i \times \sum \frac{PC_{iM.dryas}}{NP_{M.dryas}}$$

where *na* is the absolute nectar abundance of the nectar plant species *i* and *NP* is the number of nectar plant species of *M. dryas*. For each plot, the sum of weighted nectar abundances was calculated, and the mean value for the two visits to each plot was built (Fartmann et al. 2013).

Oviposition habitat

To determine oviposition habitat requirements, egg-laying females were tracked during July and August in the plot with the highest adult abundance, a calcareous fen within a common pasture. In case of oviposition, we searched for the eggs after deposition and the location was marked. To describe vegetation structure and microclimatic conditions, we recorded the same parameters considered for the adult habitats, except nectar abundance, in a radius of 30 cm around the oviposition and random sites, respectively (Streitberger et al. 2012; Weking et al. 2013). Random sites were selected by a randomly thrown stick (Anthes et al. 2003). The ratio between oviposition and random sites was 2 : 1 ($n = 22$ vs. $n = 11$).

Statistical analysis

Differences in absolute frequencies of nominal environmental variables were tested using the Chi-squared test. To assess differences of numerical environmental variables between common-pasture and control plots, occupied and unoccupied plots and oviposition and random sites, we used generalised linear mixed-effects models (GLMM) with *subarea* as a random factor (error structure: binomial, negative binomial and Poisson, respectively). Differences in numerical environmental variables and the abundance of *M. dryas* between the three different land-use types (fallow, mown once, mown twice or more often) of control plots, as well as the abundance of *M. dryas* between common-pasture and control plots were tested in the same way. In case of overdispersion, we set up an observation-level random intercept nested in the *subarea* the GLMM. All pairwise comparisons between land-use types were made using the function ‘glht()’ in the multcomp package (Hothorn et al. 2008) and the default ‘single-step’ method to adjust the *P* values for multiple testing.

To analyse the effects of environmental parameters on plot-occupancy (binomial response variable) and abundance (negative binomial response variable) of *M. dryas*, we conducted GLMM with *subarea* as a random factor. To avoid multi-collinearity (Graham 2003; Löffler and Fartmann 2017), we calculated Spearman rank correlations (r_s) prior to the GLMM analysis and excluded parameters with strong intercorrelations ($|r_s| \geq 0.5$) (Appendix Table A1). To identify the most important parameters and increase model robustness, model averaging based on an information-theoretic approach (Burnham and Anderson 2002; Grueber et al. 2011) was conducted. Model averaging was calculated using the *dredge* function (R package MuMIn; Bartón 2016) and only included top-ranked models within $\Delta AIC_C < 3$ (Grueber et al. 2011). The explanatory power of the models is shown by the range of marginal (R^2_M) and conditional (R^2_C) R^2 values of the top-ranked models (Nakagawa and Schielzeth 2013; Nakagawa et al. 2017). All statistical analyses were performed with R 2.15.0 (R Development Core Team 2018).

Results

Plots

The four vegetation types occurring at the plots were equally distributed across common pastures and control plots and did not differ between the two plot types (Appendix Table A2). At common pastures and control plots, fens, raised bogs and grasslands on mineral soil covered in each case approximately one-quarter of the plots. About one-fifth of the

plots were transition mires. In contrast, land use differed between the common pastures and control plots (Appendix Table A2). All common pastures were grazed, whereas none of the control plots was used as pasture. Nearly half of the control plots were fallows and 38% were mown once (litter meadows). The remaining 13% of the plots were more intensively used meadows (mown twice or even more often).

Due to the differences in land use, common pastures had denser vegetation in 25–30 cm height from the ground, lower cover of herbs and higher nectar abundance than control plots (Appendix Table A3). All other numerical parameters did not differ between common pastures and control plots. Within the control plots, land-use also strongly affected vegetation structure and nectar abundance. Fallows and meadows mown once especially differed from the more intensively used meadows. Fallows had the highest cover of shrubs and herbs differing from the two other land-use types. The cover of litter was highest and cover of Poaceae was lowest on fallows and plots mown once compared with plots mown twice or more often. The cover of mosses decreased from fallows over plots mown once to intensively used meadows. The cover of sedges and nectar abundance were highest at litter meadows differing from at least one of the two other land-use types. All other numerical parameters did not differ among the three land-use types of control.

Adult habitat

Altogether, we recorded 575 adult *M. dryas* individuals in 74 (67%) of the 110 plots that were studied. Plot occupancy was equal in common pastures and control plots with two-thirds (67.3%) of the plots being colonised in each case.

Both vegetation and land-use type affected the plot occupancy of *M. dryas* (Table 1). Fens and transition mires were strongly preferred. Except one plot in a transition mire, all plots belonging to these two vegetation types were occupied. Grasslands on mineral soil were also important habitats of

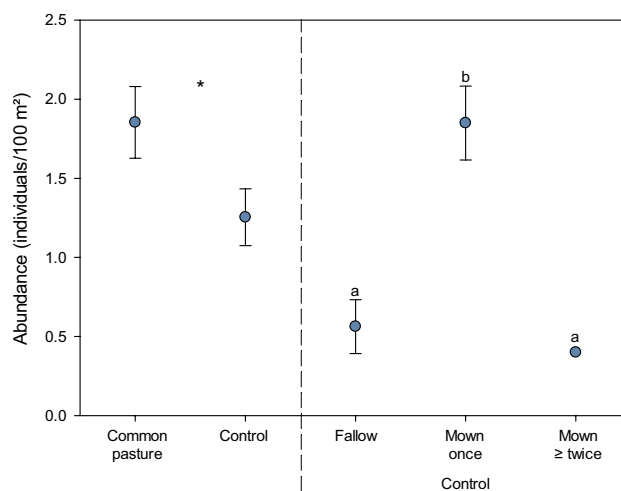


Fig. 3 Abundance of *Minois dryas* (mean ± SE) in occupied common-pastures and control plots. Differences were tested using generalized linear mixed-effect models (GLMM) with *subarea* as a random factor. In case of over-dispersion, we set up an observation-level random intercept nested in the *subarea*. For further details see *Statistical analysis*. * $P < 0.05$. Different letters indicate significant differences between land-use types

M. dryas, with 60% of all studied grasslands being occupied. This was especially true for common pastures; here, 65% of all occupied grasslands on mineral soil were situated. In contrast, raised bogs were rarely colonised; *M. dryas* was present only in 20% of the raised bog plots. Regarding land use, plots mown once (litter meadows) (plot occupancy: 95%) and pastures (67%) were preferred by *M. dryas*, whereas intensively used grasslands (14%) were avoided.

The abundance of *M. dryas* in occupied plots was higher in common pastures compared with control plots (Fig. 3). However, at control, the abundance of *M. dryas* in occupied plots was affected by land use. Abundance was highest at plots mown once (litter meadows) and lowest at intensively used plots and fallows.

Table 1 Absolute and relative frequencies of vegetation and land-use type at occupied ($n = 74$) and unoccupied plots ($n = 36$) of *Minois dryas*. Differences were tested using the Chi-squared test. *** $P < 0.001$

Parameter	Occupied		Unoccupied		Chi	df	P
	n	%	n	%			
Vegetation type					53.5	3	***
Fen	31	41.9	0	0			
Raised bog	6	8.1	24	66.7			
Grassland	17	23.0	11	30.6			
Transition mire	20	27.0	1	2.8			
Land-use type					17.2	3	***
Fallow	16	21.6	11	30.6			
Mown once	20	27.0	1	2.8			
Mown ≥ twice	1	1.4	6	16.7			
Pasture	37	50.0	18	50.0			

Table 2 Mean values (\pm SE) of numerical parameters at occupied and unoccupied plots of *Minois dryas* in all plots ($n_{occupied}=74$ vs. $n_{unoccupied}=36$) and common pastures ($n_{occupied}=37$ vs. $n_{unoccupied}=18$). Differences were tested using generalized linear mixed-effect models (GLMM) with *subarea* as a random factor. In case of over-dispersion, we set up an observation-level random intercept nested in the *subarea*. For further details see *Statistical analysis*. Error structure is marked with superscript letters behind the *P* values: *b* binomial, *nb* negative binomial, *p* Poisson. n.s. = not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Parameter	All plots		<i>P</i>	Common pasture		<i>P</i>
	Occupied	Unoccupied		Occupied	Unoccupied	
Vegetation height (cm) ^a	15.7 \pm 1.1	12.3 \pm 1.2	*** <i>P</i>	17.9 \pm 1.6	9.4 \pm 0.7	*** <i>nb</i>
Vegetation density (%) ^b						
10–15 cm height	48.4 \pm 4.3	30.8 \pm 5.6	*** <i>b</i>	60.3 \pm 5.5	23.1 \pm 6.7	*** <i>b</i>
25–30 cm height	9.8 \pm 2.2	5.8 \pm 2.7	*** <i>b</i>	14.7 \pm 3.8	1.8 \pm 1.4	*** <i>b</i>
Cover (%) of						
Shrubs	6.5 \pm 1.6	17.0 \pm 2.7	*** <i>b</i>	4.7 \pm 1.7	22.9 \pm 3.8	*** <i>b</i>
Poaceae	27.5 \pm 2.6	43.8 \pm 3.1	* <i>b</i>	26.7 \pm 3.7	38.3 \pm 3.4	n.s. ^{<i>b</i>}
Sedges	34.2 \pm 2.5	1.3 \pm 1.1	*** <i>b</i>	40.8 \pm 3.6	0.3 \pm 0.3	*** <i>b</i>
Rushes	3.5 \pm 0.6	0.4 \pm 0.3	*** <i>b</i>	3.6 \pm 0.8	0.5 \pm 0.4	*** <i>b</i>
Herbs	26.5 \pm 1.8	39.6 \pm 3.4	n.s. ^{<i>b</i>}	20.6 \pm 1.8	35.3 \pm 4.3	* <i>b</i>
Mosses	85.0 \pm 2.9	71.1 \pm 7.2	n.s. ^{<i>b</i>}	80.8 \pm 5.0	81.4 \pm 8.5	n.s. ^{<i>b</i>}
Open soil	1.5 \pm 0.2	1.1 \pm 0.4	n.s. ^{<i>b</i>}	2.1 \pm 0.3	0.2 \pm 0.1	*** <i>b</i>
Litter	13.4 \pm 1.9	7.7 \pm 0.8	n.s. ^{<i>b</i>}	15.3 \pm 3.4	9.5 \pm 1.1	*** <i>b</i>
Nectar abundance (10 m ²) ^c	11.1 \pm 1.8	3.0 \pm 0.7	*** <i>nb</i>	14.8 \pm 3.3	4.6 \pm 1.4	* <i>nb</i>
Sunshine duration (h) ^d	11.5 \pm 0.2	11.4 \pm 0.3	n.s. ^{<i>P</i>}	11.7 \pm 0.3	11.3 \pm 0.3	n.s. ^{<i>nb</i>}
Dropping density (no./100 m ²)						
Cow pats				1.3 \pm 0.3	0.8 \pm 0.4	*** <i>nb</i>
Horse dropping				0.3 \pm 0.1	0.0 \pm 0.0	* <i>P</i>

^aMeasured three times at a randomly chosen location in the study plot, here mean value is calculated

^bMeasured within a frame of 30 cm depth and 50 cm width above ground (Poniatowski and Fartmann 2008)

^cSee *Statistical analysis*

^dMeasured for the month of August in the centre of the plot with a horizontoscope after Tonne (1954), accuracy ½ h

The habitat characteristics of plots occupied and unoccupied by *M. dryas* differed, as well as in both general and common pastures (Table 2). However, the patterns for all plots and common pastures were quite similar. Occupied plots had higher and denser vegetation, lower cover of shrubs, higher cover of sedges and rushes, and higher nectar abundance. Regarding all plots, occupied ones had also a lower cover of Poaceae. At common pastures, occupied plots, additionally, had a lower cover of herbs, more open soil and litter and a higher grazing intensity (cow-pat and horse-dropping density).

At all plots, the likelihood of plot occupancy by *M. dryas* increased with the cover of sedges and nectar abundance (Table 3a). Within occupied plots, the abundance of *M. dryas* decreased with the cover of shrubs and increased with vegetation density (in 10–15 cm height from the ground) (Table 3b). At common pastures, the likelihood of occurrence of *M. dryas* increased with the cover of sedges (Table 4a). At occupied plots within common pastures, the abundance of *M. dryas* increased with the cover of sedges and rushes, as well as with vegetation density (in 10–15 cm height from the ground) (Table 4b).

Oviposition habitat

Oviposition habitats in the plot with the highest adult abundance in common pastures, a calcareous fen, were characterised by a short but dense and heterogeneous sward with a very high cover of mosses, a well-developed layer of sedges and some litter (Table 5). None of the environmental parameters differed between the oviposition and random sites.

Discussion

Our study revealed that plot occupancy was equal at common pastures and control plots. However, the abundance of *M. dryas* was higher at common pastures, although the composition of vegetation types did not differ between the two plot types. Fens and transition mires, traditionally managed as common pastures or litter meadows, were the preferred habitats of *M. dryas*. The cover of sedges was the key driver of plot occupancy and abundance (only in common pastures).

Table 3 Model-averaging results (GLMM) of the relationship between a) plot-occupancy ($n_{occupied}=74$ vs. $n_{unoccupied}=36$) of *Minois dryas* (binomial response variable) and environmental parameters as well as b) abundance of *M. dryas* in occupied plots ($n=74$; negative binomial response variable) and environmental parameters. For all models model-averaged coefficients (full average) were derived from the top-ranked model ($\Delta AIC_c < 3$). The explanatory power of the models is shown by the range of marginal (R^2_M) and conditional (R^2_C) R^2 values of the top-ranked models (Nakagawa and Schielzeth 2013; Nakagawa et al. 2017). For further details see *Statistical analysis*. n.s. = not significant, * $P < 0.05$, *** $P < 0.001$

Parameter	Estimate	SE	Z	P
a) Plot-occupancy model ^{1,2}				
(Intercept)	3.03	2.25	1.34	n.s
Cover of sedges	0.20	0.05	3.69	***
Nectar abundance	0.15	0.07	2.15	*
Sunshine duration	0.02	0.08	0.25	n.s
Cover of shrubs	-0.01	0.02	0.63	n.s
Cover of herbs	0.00	0.01	0.30	n.s
Cover of rushes	0.01	0.06	0.19	n.s
Cover of open soil	-0.04	0.12	0.34	n.s
Cover of litter	0.00	0.02	0.05	n.s
Vegetation density 10–15 cm height	0.00	0.00	0.00	n.s
$R^2_M=0.83-0.85$, $R^2_C=0.83-0.85$				
b) Abundance model ^{3,4}				
(Intercept)	1.51	0.41	3.63	***
Cover of shrubs	-0.02	0.01	2.36	*
Vegetation density 10–15 cm height	0.01	0.00	4.07	***
Cover of sedges	0.01	0.01	1.24	n.s
Cover of herbs	-0.01	0.01	1.25	n.s
$R^2_M=0.55-0.60$, $R^2_C=0.50-0.52$				

¹Parameters that were excluded due to strong intercorrelations: Vegetation height, vegetation density 25–30 cm height, cover of Poaceae and cover of mosses (Appendix Table A1)

²Variables not included top-ranked models with $\Delta AIC_c < 3$: Cover of litter

³Parameters that were excluded due to strong intercorrelations: Vegetation height, vegetation density 25–30 cm height, cover of Poaceae, cover of mosses and cover of litter (Appendix Table A1)

⁴Variables not included in top-ranked models with $\Delta AIC_c < 3$: Cover of rushes, cover of open soil, nectar abundance and sunshine duration

The observed preference of *M. dryas* for fens and transition mires in the northern pre-Alps is in line with former observations (Sachteleben and Winterholler 2013; Hermann 2020). Fens and transition mires that are traditionally used as litter meadows are known to host abundant populations of *M. dryas* (Sachteleben and Winterholler 2013). However, the effects of grazing on *M. dryas* populations in mires have so far been controversially discussed (see *Introduction*). In contrast, our study showed that the abundance of *M. dryas* in

Table 4 Model-averaging results (GLMM) of the relationship between a) plot-occupancy ($n_{occupied}=37$ vs. $n_{unoccupied}=18$) of *Minois dryas* (binomial response variable) and environmental parameters at common pastures as well as b) abundance of *M. dryas* at occupied plots ($n=37$; negative binomial response variable) and environmental parameters at common pastures. For all models model-averaged coefficients (full average) were derived from the top-ranked model ($\Delta AIC_c < 3$). The explanatory power of the models is shown by the range of marginal (R^2_M) and conditional (R^2_C) R^2 values of the top-ranked models (Nakagawa and Schielzeth 2013; Nakagawa et al. 2017). For further details see *Statistical analysis*. n.s. = not significant, * $P < 0.05$, ** $P < 0.01$

Parameter	Estimate	SE	Z	P
a) Plot-occupancy model ^{1,2}				
(Intercept)	-2.23	0.89	2.48	*
Cover of sedges	0.49	0.16	3.08	**
Nectar abundance	0.06	0.08	0.74	n.s
$R^2_M=0.96-0.97$, $R^2_C=0.96$				
b) Abundance model ^{3,4}				
(Intercept)	0.99	0.35	2.75	**
Cover of sedges	0.01	0.01	2.24	*
Cover of rushes	0.06	0.02	2.62	**
Vegetation density 10–15 cm height	0.01	0.00	2.28	*
$R^2_M=0.41-0.48$, $R^2_C=0.52-0.56$				

¹Parameters that were excluded due to strong inter-correlations: Vegetation height, vegetation density in 25–30 cm height, cover of shrubs, cover of Poaceae, cover of rushes, cover of herbs, cover of mosses and density of cow pats (Appendix Table A1)

²Variables not included in top-ranked models with $\Delta AIC_c < 3$: vegetation density 10–15 cm height, cover of litter, cover of open soil, sunshine duration and horse-dropping density

³Parameters that were excluded due to strong intercorrelations: Vegetation height, vegetation density 25–30 cm height, cover of shrubs, cover of Poaceae, cover of mosses and cover of litter (Appendix Table A1)

⁴Variables not included in top-ranked models with $\Delta AIC_c < 3$: Cover of herbs, cover of open soil, nectar abundance, sunshine duration, cow-pat density and horse-dropping density

common pastures can be as high as those in litter meadows. Additionally, at common pastures, occupied plots even had a higher density of cow pats and horse droppings compared with unoccupied plots, indicating that those parts of the pastures with a higher grazing intensity were even preferred by *M. dryas*.

A high cover of sedges is characteristic for fens and transition mires (Dierßen and Dierßen 2008; Ellenberg and Leuschner 2010; own observation). Hence, the positive relationship between plot occupancy or abundance of *M. dryas* and the cover of sedges underlines the general significance of these two vegetation types for the butterfly species.

Table 5 Mean values (\pm SE) of numerical parameters at oviposition ($n=22$) and random sites ($n=11$) of *Minois dryas* in a calcareous fen within a common pasture. Differences were tested using generalized linear mixed-effect models (GLMM) with *subarea* as a random factor. In case of over-dispersion, we set up an observation-level random intercept nested in the *subarea*. For further details see *Statistical analysis*. Error structure is marked with superscript letters behind the *P* values: *b* binomial, *nb* negative binomial. n.s. = not significant

Parameter	Oviposition site	Random site	<i>P</i>
Vegetation height (cm) ^a	13.8 \pm 1.0	13.4 \pm 1.8	n.s. ^{nb}
Vegetation density (%) ^b			
10–15 cm height	54.1 \pm 6.0	50.0 \pm 8.1	n.s. ^b
25–30 cm height	6.4 \pm 2.1	4.3 \pm 1.8	n.s. ^b
Cover (%) of			
Poaceae	34.8 \pm 4.1	43.0 \pm 7.0	n.s. ^b
Sedges	30.4 \pm 3.3	25.9 \pm 3.2	n.s. ^b
Rushes	6.6 \pm 3.4	0.5 \pm 0.5	n.s. ^b
Herbs	19.6 \pm 2.5	21.6 \pm 6.9	n.s. ^b
Mosses	95.7 \pm 2.1	91.2 \pm 5.6	n.s. ^b
Litter	15.6 \pm 4.1	15.7 \pm 5.1	n.s. ^b
Sunshine duration (h) ^c	10.4 \pm 0.2	11.0 \pm 0.4	n.s. ^{nb}

^aMeasured three times at a randomly chosen location in the plot

^bMeasured within a frame of 30 cm depth and 50 cm width above ground (Poniatowski and Fartmann 2008)

^cMeasured for the month of August in the centre of the plot with a horizonscope after Tonne (1954), accuracy ½ h

In addition, sedges are important host plants for the egg-dropping species (see *Study species*). Therefore, the cover of sedges is also a proxy for the availability of sufficient host plants. Freshly hatched caterpillars have to actively locate their food source. Consequently, to avoid the time-consuming searching behaviour of the sensitive larvae, it is a general rule that egg-dropping butterflies depend on dense stands of their host plants (Wiklund 1984; Streitberger et al. 2012). In contrast, Poaceae, the second important group of host plants (see Sect. 2.2), were hardly a limiting factor for patch occupancy and abundance. Poaceae had a high cover across all plots (Appendix Table A3) and were always negatively correlated with the cover of sedges (Appendix Table A1).

Most studied plots, except some improved grasslands, were nutrient-poor (see *Study area*; own observation) and, accordingly, had a relatively low vegetation height and density (Appendix Table A3). *Minois dryas*, however, is known to avoid very short vegetation, even when sufficient host

plants are present (Sachteleben and Winterholler 2013). In line with this, the abundance of the species increased at occupied plots (all plots, common pastures) with vegetation density, which was intercorrelated with vegetation height (Appendix Table A1).

Grasslands on mineral soil usually have a low significance as habitats for *M. dryas* in the northern pre-Alps (Ebert and Rennwald 1991; Sachteleben and Winterholler 2013). However, in our study, these grasslands were regularly colonised by *M. dryas*, especially at common pastures. There are two possible explanations for the observed pattern: (i) adults from adjacent fens and transition mires used nectar resources in these grasslands for feeding or (ii) *M. dryas* was, additionally, even able to reproduce here. Indeed the distances between grasslands on mineral soil and the two main habitats, fens and transition mires, were often low (see *Study area*; Schwarz et al. 2018). Moreover, sufficient nectar resources are known to play a decisive role for adults (e.g., Kalarus et al. 2013; Akeboshi et al. 2015; Kalarus and Nowicki 2017). In line with the latter, the nectar abundance at occupied plots was higher compared to those of unoccupied ones and the likelihood of patch occupancy at all plots increased with nectar abundance. In common pastures, grasslands on mineral soil were often characterised by some ruderal patches rich in tall forbs, such as *Eupatorium cannabinum* or thistles (*Cirsium* spp.), that were very important spots for food intake of *M. dryas* (own observation). Additionally, in particular, very wet or water-logged parts of these grasslands had a moisture and cover of sedges comparable to those of fens or transition mires (own observation). Consequently, reproduction might also be possible in such grasslands.

Rushes are typical of fens and transition mires, although with a much lower cover than sedges (Dierßen and Dierßen 2008; Ellenberg and Leuschner 2010; own observation). Additionally, rushes regularly occurred at wet or water-logged parts of the grasslands on mineral soil in the common pastures (own observation). Hence, the positive relationship between the plot occupancy (all plots) and abundance (occupied plots: common pastures) of *M. dryas* and the cover of rushes underpins the preference not only for fens and transition mires but also for the wettest grasslands on mineral soils in common pastures.

Raised bogs are known to generally have a low importance for *M. dryas* (Sachteleben and Winterholler 2013),

which was in line with our study. Many sufficient habitat requirements (e.g. high cover of host plants, tall vegetation or sufficient nectar resources) are not fulfilled (see above; own observation).

M. dryas is known to occur also along grassland-forest edges or even in light woodlands (Sachteleben and Winterholler 2013; Akeboshi et al. 2015). However, as our study showed, too much shading through shrubs results in decreasing abundance and even the disappearance of the species.

At control, both fallows and intensively used meadows were largely unsuitable for *M. dryas*. They had a low nectar abundance (Appendix Table A3). Additionally, fallows were characterised by a high cover of shrubs, and in intensively used meadows, even fundamental requirements, such as *Carex* host plants, were completely lacking.

Habitat structures at oviposition and random sites in a calcareous fen did not differ in our study. As the fen was characterised by a short but dense sward with a well-developed layer of sedges and some litter, we suspect that it offered generally suitable conditions for reproduction, explaining the lack of difference. The plot had the highest adult abundance in common pastures, which provides further evidence for this assumption.

To sum up, open fens and transition mires traditionally managed as common pastures or litter meadows were the main habitats of *M. dryas* in our study area in the northern pre-Alps. They offered (i) sufficient host plants (*Carex* spp.), (ii) high availability of nectar resources, and (iii) vegetation that was neither too sparse nor too short. In contrast, both abandonment and intensive land use had negative impacts on the occurrence of the endangered butterfly species.

Implications for conservation

Within common pastures, stocking capacities ranged from 0.5–2.0 livestock units per hectare (see *Study species*). However, real grazing intensity within the pastures usually depends on the productivity of the vegetation type (Lederbogen et al. 2004). Especially in raised bogs and to a lesser extent in transition mires, they are usually under the lower end of the mentioned range. In contrast, in the areas with fertilised grasslands on mineral soils, cows and horses spend

a lot of time grazing, and local stocking rates may even be above the upper end of the range. Based on our study and other recent research from the common pastures, we recommend to maintain the current grazing regime to foster biodiversity in general (Lederbogen et al. 2004; Weking et al. 2013; Schwarz et al. 2018) and *M. dryas* in particular. Additionally, where possible, abandoned fens and transition mires adjacent to common pastures should be integrated into the low-intensity pasture systems.

The preservation of traditionally managed litter meadows is the second important possibility to conserve *M. dryas* populations in the study area. Prior studies have already shown that many other rare insect species benefit from this type of management (Anthes et al. 2003; Lederbogen et al. 2004; Settele et al. 2009; Weking et al. 2013).

All habitats of *M. dryas* were characterised by relatively high water tables. Hence, conservation management should aim to maintain high water levels or restore them (Settele et al. 2009; Weking et al. 2013). In general, stabilisation of the water level will increasingly become important to mitigate the effects of climate change in the future (IPBES 2019).

As is known for most butterfly species (Wilson and Roy 2009), there is evidence that *M. dryas* forms metapopulations, too (Beneš et al. 2002; Sachteleben and Winterholler 2013). Hence, patch occupancy depends not only on habitat quality but also on habitat area and isolation (Anthes et al. 2003; Eichel and Fartmann 2008; Stuhldreher and Fartmann 2014). In addition, *M. dryas* is a species with high area requirements (Sachteleben and Winterholler 2013). Accordingly, in particular, we recommend to preserve and enlarge networks of large and well-connected habitats.

In conclusion, to foster biodiversity in general and *M. dryas* in particular, we recommend to maintain and enlarge networks of large and well-connected traditionally managed (i) common pastures and (ii) litter meadows. Additionally, conservation management should aim to maintain high water levels or restore them within these habitats.

Appendix

See Table A1, A2, A3.

Table A1 Results of Spearman rank correlations (r_s). Variables with strong intercorrelations ($|r_s| \geq 0.5$) are highlighted by bold type. For further information see *Statistical analysis*. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Parameter	Density (10–15 cm)	Density (25–30 cm)	Cover of shrubs	Cover of Poaceae	Cover of sedges	Cover of rushes	Cover of herbs	Cover of mosses	Cover of litter	Cover of open soil	Nectar abundance	Sunshine duration	Cow-pat density	Horse-dropping density
All plots														
<i>Plot occupancy (Table 3a)</i>														
Vegetation height	0.80***	0.68***	-0.41***	0.32***	0.07	0.34***	-0.08	-0.33***	-0.52***	0.30**	0.50***	0.11	-	-
Density (10–15 cm)	/	0.73***	-0.39***	0.31	0.10	0.30**	-0.14	-0.28**	-0.40***	0.22*	0.44***	-0.06	-	-
Density (25–30 cm)	/	-0.36***	0.17	0.27**	0.32***	0.22*	-0.16	-0.33***	0.18	0.33***	0.05	0.05	-	-
Cover of shrubs	/	-0.31**	-0.29**	-0.39***	0.06	0.64***	0.26**	-0.28**	-0.42***	-0.30**	-	-	-	-
Cover of Poaceae	/	-0.64***	0.08	0.28**	-0.37***	0.05	0.13	-0.01	-	-	-	-	-	-
Cover of sedges	/	0.38***	-0.49***	-0.04	0.19	0.20*	0.16	0.22*	-	-	-	-	-	-
Cover of rushes	/	-0.27**	-0.26**	-0.14	0.23*	0.42	0.20*	-	-	-	-	-	-	-
Cover of herbs	/	-0.06	-0.05	-0.03	-0.02	-0.13	-	-	-	-	-	-	-	-
Cover of mosses	/	0.06	-0.54***	-0.28**	-0.35*	-	-	-	-	-	-	-	-	-
Cover of litter	/	0.13	-0.28**	0.09	-	-	-	-	-	-	-	-	-	-
Cover of open soil	/	0.18	0.23*	-	-	-	-	-	-	-	-	-	-	-
Nectar abundance	/	0.14	-	-	-	-	-	-	-	-	-	-	-	-
Sunshine duration	/	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Abundance (Table 3b)</i>														
Vegetation height	0.85***	0.74***	-0.25*	0.36**	-0.10	0.38***	-0.01	-0.14	-0.55***	0.14	0.56***	-0.00	-	-
Density (10–15 cm)	/	0.76***	-0.28*	0.42***	-0.09	0.34**	0.03	-0.13	-0.43**	0.13	0.48***	-0.10	-	-

Table A1 (continued)

Parameter	Density (10–15 cm)	Density (25–30 cm)	Cover of shrubs	Cover of Poaceae	Cover of sedges	Cover of rushes	Cover of herbs	Cover of mosses	Cover of litter	Cover of open soil	Nectar abundance	Sunshine duration	Cow-pat density	Horse-dropping density
Density (25–30 cm)	/	/	-0.21	0.22	0.09	0.27*	-0.03	-0.03	-0.33**	0.13	0.38***	-0.00	-	-
Cover of shrubs	/	/	/	-0.40***	0.01	-0.30*	-0.20	0.48***	0.27*	-0.12	-0.39***	-0.10	-	-
Cover of Poaceae	/	/	/	/	-0.66***	0.30**	0.30**	-0.36**	-0.29*	0.08	0.34	-0.13	-	-
Cover of sedges	/	/	/	/	/	0.07	-0.41***	0.06	0.28*	0.21	-0.06	0.25*	-	-
Cover of rushes	/	/	/	/	/	/	-0.14	-0.28*	-0.18	0.24*	0.32**	0.18	-	-
Cover of herbs	/	/	/	/	/	/	/	-0.11	-0.18	-0.09	0.08	-0.15	-	-
Cover of mosses	/	/	/	/	/	/	/	/	-0.09	-0.60***	-0.26	-0.23*	-	-
Cover of litter	/	/	/	/	/	/	/	/	/	0.21	-0.50***	0.18	-	-
Cover of open soil	/	/	/	/	/	/	/	/	/	/	0.14	0.27*	-	-
Nectar abundance	/	/	/	/	/	/	/	/	/	/	/	0.00	-	-
Sunshine duration	/	/	/	/	/	/	/	/	/	/	/	/	-	-
Common-pasture plots														
<i>Plot occupancy (Table 4a)</i>														
Vegetation height	0.74***	0.67***	-0.49**	0.02	0.43**	0.55***	-0.13	-0.33*	-0.36**	0.53***	0.55***	0.16	0.43**	-0.08
Density (10–15 cm)	/	0.72***	-0.55***	0.04	0.45***	0.46	-0.12	-0.30*	-0.24	0.40**	0.48***	0.08	0.47***	-0.01
Density (25–30 cm)	/	/	-0.41**	-0.11	0.56***	0.48	-0.24	-0.13	-0.29*	0.34*	0.35**	0.15	0.41**	0.00
Cover of shrubs	/	/	/	-0.27	-0.34*	-0.43**	-0.02	0.66***	0.12	-0.35**	-0.56***	-0.28*	-0.79***	-0.19

Table A1 (continued)

Parameter	Density (10–15 cm)	Density (25–30 cm)	Cover of shrubs	Cover of Poaceae	Cover of sedges	Cover of rushes	Cover of herbs	Cover of mosses	Cover of litter	Cover of open soil	Nectar abundance	Sunshine duration	Cow-pat density	Horse-dropping density
Cover of Poaceae			/	/	-0.63***	0.21	0.35**	-0.34*	0.14	0.01	0.13	-0.14	0.26	-0.13
Cover of sedges			/		/	0.32*	-0.51***	-0.10	0.02	0.38**	0.14	0.28*	0.21	0.37**
Cover of rushes					/	/	-0.29*	-0.44***	-0.22	0.57***	0.43**	0.27*	0.40**	-0.04
Cover of herbs						/	/	-0.11	0.04	-0.12	0.21	-0.10	0.09	-0.06
Cover of mosses							/	/	-0.13	-0.60***	-0.52***	-0.39**	-0.76***	-0.20
Cover of litter									/	0.04	-0.33*	0.20	-0.06	0.49***
Cover of open soil										/	0.39**	0.38**	0.40**	0.24
Nectar abundance											/	0.14	0.57***	-0.13
Sunshine duration												/	0.30*	0.10
Cow-pat density													/	-0.01

Table A1 (continued)

Parameter	Density (10–15 cm)	Density (25–30 cm)	Cover of shrubs	Cover of Poaceae	Cover of sedges	Cover of rushes	Cover of herbs	Cover of mosses	Cover of litter	Cover of open soil	Nectar abundance	Sunshine duration	Cow-pat density	Horse-dropping density
<i>Abundance (Table 4b)</i>														
Vegetation height	0.79***	0.68***	-0.20	0.16	0.00	0.42**	0.15	-0.08	-0.50***	0.30	0.51***	-0.01	0.21	-0.35
Density (10–15 cm)	/	0.69***	-0.32	0.20	0.07	0.37*	0.26	-0.08	-0.25	0.25	0.43**	-0.02	0.30	-0.25
Density (25–30 cm)	/	/	-0.15	-0.02	0.26	0.29	0.08	0.06	-0.28	0.17	0.41*	-0.06	0.30	-0.21
Cover of shrubs	/	/	/	-0.49**	0.23	-0.10	-0.38*	0.41*	0.19	0.01	-0.38*	0.04	-0.66***	-0.03
Cover of Poaceae	/	/	/	/	-0.73***	0.34*	0.40*	-0.48**	-0.13	0.16	0.19	-0.24	0.46**	0.07
Cover of sedges	/	/	/	/	/	-0.07	-0.39*	0.34*	0.23	0.01	-0.09	0.24	-0.28	0.22
Cover of rushes	/	/	/	/	/	/	-0.19	-0.23	-0.15	0.44**	0.31	0.16	0.17	-0.23
Cover of herbs	/	/	/	/	/	/	/	-0.41*	-0.20	0.08	0.44**	-0.09	0.47**	0.08
Cover of mosses	/	/	/	/	/	/	/	/	-0.11	-0.55***	-0.34*	-0.17	-0.64***	-0.11
Cover of litter	/	/	/	/	/	/	/	/	/	0.11	-0.57***	0.19	-0.13	0.62***
Cover of open soil	/	/	/	/	/	/	/	/	/	/	0.18	0.32	0.23	0.12
Nectar abundance	/	/	/	/	/	/	/	/	/	/	/	-0.07	0.47**	-0.28
Sunshine duration	/	/	/	/	/	/	/	/	/	/	/	/	0.04	0.03
Cow-pat density	/	/	/	/	/	/	/	/	/	/	/	/	/	-0.14

Table A2 Absolute and relative frequencies of vegetation and land-use type at common-pastures ($n=55$) and control plots ($n=55$). Differences were tested using the Chi-squared test. n.s. = not significant, *** $P < 0.001$

Parameter	Common pasture		Control		Chi	df	P
	n	%	n	%			
Vegetation type					0.2	3	n.s
Fen	15	27.3	16	29.1			
Raised bog	15	27.3	15	27.3			
Grassland	15	27.3	13	23.6			
Transition mire	10	18.2	11	20.0			
Land-use type					110.0	3	***
Fallow	.	.	27	49.1			
Mown once	.	.	21	38.2			
Mown \geq twice	.	18.2	7	12.7			
Pasture	55	100	.	.			

Table A3 Mean values (\pm SE) of numerical parameters at common-pastures ($n=55$) and control plots ($n=55$), respectively, and the three land-use types at control plots ($n_{\text{fallow}}=27$ vs. $n_{\text{mown once}}=21$ vs. $n_{\text{mown } \geq \text{twice}}=7$). Differences between common-pastures and control plots and between the three land-use types at control were tested using generalized linear mixed-effect models (GLMM) with *subarea*

as a random factor. In case of over-dispersion, we set up an observation-level random intercept nested in the *subarea*. For further details see *Statistical analysis*. Error structure is marked with superscript letters behind the *P* values: *b* binomial, *nb* negative binomial, *p* Poisson. n.s. = not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Parameter	Common pasture	Control	P	Control			P
				Fallow	Mown once	Mown \geq twice	
Vegetation height (cm) ^a	15.1 \pm 1.2	14.0 \pm 1.2	n.s. ^p	12.0 \pm 1.5	13.0 \pm 1.6	24.9 \pm 2.9	n.s. ^p
Vegetation density (%) ^b							
10–15 cm height	48.1 \pm 4.9	37.2 \pm 4.9	n.s. ^b	26.4 \pm 5.6	37.8 \pm 8.1	77.1 \pm 12.5	n.s. ^b
25–30 cm height	10.5 \pm 2.7	6.5 \pm 2.2	*** ^b	4.6 \pm 2.8	2.4 \pm 0.9	26.1 \pm 11.0	n.s. ^b
Cover (%) of							
Shrubs	10.7 \pm 2.1	9.3 \pm 2.0	n.s. ^b	18.9 \pm 3.3 ^a	0.0 \pm 0.0 ^b	0.0 \pm 0.0 ^b	*** ^b
Poaceae	30.5 \pm 2.8	35.1 \pm 3.2	n.s. ^b	31.4 \pm 4.1 ^a	29.5 \pm 4.8 ^a	66.1 \pm 3.0 ^b	*** ^b
Sedges	27.5 \pm 3.5	19.4 \pm 2.8	n.s. ^b	13.6 \pm 3.4 ^a	33.2 \pm 4.3 ^b	0.0 \pm 0.0 ^a	*** ^b
Rushes	2.6 \pm 0.6	2.4 \pm 0.7	n.s. ^b	1.3 \pm 0.8	4.5 \pm 1.3	0.0 \pm 0.0	n.s. ^b
Herbs	25.4 \pm 2.1	36.1 \pm 2.7	*** ^b	44.3 \pm 4.7 ^a	28.6 \pm 2.1 ^b	27.1 \pm 2.1 ^b	* ^b
Mosses	81.0 \pm 4.3	79.9 \pm 4.5	n.s. ^b	95.9 \pm 1.8 ^a	85.0 \pm 4.8 ^b	2.4 \pm 0.6 ^c	* ^b
Open soil	1.5 \pm 0.3	1.3 \pm 0.3	n.s. ^b	1.2 \pm 0.6	1.3 \pm 0.5	1.7 \pm 0.4	n.s. ^b
Litter	13.4 \pm 1.6	9.7 \pm 1.3	n.s. ^b	11.6 \pm 1.4 ^a	10.1 \pm 2.7 ^a	1.1 \pm 0.8 ^b	* ^b
Nectar abundance (10 m ²) ^c	11.5 \pm 2.3	5.4 \pm 1.0	** ^{nb}	2.5 \pm 0.7 ^a	9.9 \pm 2.2 ^b	3.0 \pm 1.6 ^{ab}	*** ^b
Sunshine duration (h) ^d	11.6 \pm 0.2	11.3 \pm 0.3	n.s. ^p	11.1 \pm 0.4	11.6 \pm 0.4	11.4 \pm 1.2	n.s. ^p

^aMeasured three times at a randomly chosen location in the plot

^bMeasured within a frame of 30 cm depth and 50 cm width above ground (Poniatowski and Fartmann 2008)

^cSee [Statistical analysis](#)

^dMeasured for the month of August in the centre of the plot with a horizonscope after Tonne (1954), accuracy $\frac{1}{2}$ h

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