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...
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 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; Sachteleben 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 (Sachteleben 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 (Sachteleben 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.
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 have 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 (= ombro-trophic 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 dura-
tion during the flight period in August was measured with
a horizontoscope 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 lit-
erature 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
(NAi) of the nectar plant species i, we used the following
formula (Fartmann et al. 2013):

\[ NA_i = na_i \times \frac{\sum PC_{i,M.\ dryas}}{NP_{M.\ dryas}} \]

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 abun-
dances 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 (Stre-
tibergen 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 environ-
mental 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 sub-
area as a random factor (error structure: binomial, negative
binomial and Poisson, respectively). Differences in numeri-
cal 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 over-
dispersion, we set up an observation-level random intercept
nested in the subarea the GLMM. All pairwise compari-
sions 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 abun-
dance (negative binomial response variable) of M. dryas,
we conducted GLMM with subarea as a random factor. To
avoid multi-collinearity (Graham 2003; Löffler and Fart-
mann 2017), we calculated Spearman rank correlations (r)
before the GLMM analysis and excluded parameters with
strong intercorrelations (|r| ≥ 0.5) (Appendix Table A1). To
identify the most important parameters and increase model
robustness, model averaging based on an information-theo-
retic 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 Δ AICc < 3 (Grue-
ber et al. 2011). The explanatory power of the models is
shown by the range of marginal \( R^2_M \) and conditional \( R^2_C \)
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 approxi-
mately 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 other two 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 *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.

![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](#).

### 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    |         |            |     |    |     |
| 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      |         |            |     |    | *** |
| 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 |    |
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).

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**Table 2** Mean values (± 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 | | | Common pasture | | |
|-----------|----------|----------|----------|-----------------|----------|
|           | Occupied | Unoccupied | *P* | Occupied | Unoccupied | *P* |
| Vegetation height (cm) | 15.7 ± 1.1 | 12.3 ± 1.2 | ***p | 17.9 ± 1.6 | 9.4 ± 0.7 | ***ab |
| Vegetation density (%) | | | | | | |
| 10–15 cm height | 48.4 ± 4.3 | 30.8 ± 5.6 | ***b | 60.3 ± 5.5 | 23.1 ± 6.7 | ***ab |
| 25–30 cm height | 9.8 ± 2.2 | 5.8 ± 2.7 | ***b | 14.7 ± 3.8 | 1.8 ± 1.4 | ***ab |
| Cover (%) of | | | | | | |
| Shrubs | 6.5 ± 1.6 | 17.0 ± 2.7 | ***b | 4.7 ± 1.7 | 22.9 ± 3.8 | ***b |
| Poaceae | 27.5 ± 2.6 | 43.8 ± 3.1 | eb | 26.7 ± 3.7 | 38.3 ± 3.4 | n.s. |
| Sedges | 34.2 ± 2.5 | 1.3 ± 1.1 | ***b | 40.8 ± 3.6 | 0.3 ± 0.3 | ***b |
| Rushes | 3.5 ± 0.6 | 0.4 ± 0.3 | ***b | 3.6 ± 0.8 | 0.5 ± 0.4 | ***ab |
| Herbs | 26.5 ± 1.8 | 39.6 ± 3.4 | n.s. | 20.6 ± 1.8 | 35.3 ± 4.3 | ab |
| Mosses | 85.0 ± 2.9 | 71.1 ± 7.2 | n.s. | 80.8 ± 5.0 | 81.4 ± 8.5 | n.s. |
| Open soil | 1.5 ± 0.2 | 1.1 ± 0.4 | n.s. | 2.1 ± 0.3 | 0.2 ± 0.1 | ****ab |
| Litter | 13.4 ± 1.9 | 7.7 ± 0.8 | n.s. | 15.3 ± 3.4 | 9.5 ± 1.1 | ****ab |
| Nectar abundance (10 m²) | 11.1 ± 1.8 | 3.0 ± 0.7 | ***ab | 14.8 ± 3.3 | 4.6 ± 1.4 | *ab |
| Sunshine duration (h) | 11.5 ± 0.2 | 11.4 ± 0.3 | n.s. | 11.7 ± 0.3 | 11.3 ± 0.3 | n.s. |

* Measure three times at a randomly chosen location in the study plot, here mean value is calculated.

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

*See Statistical analysis

*Measured for the month of August in the centre of the plot with a horizontoscope after Tonne (1954), accuracy ½ h
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 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 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 (Δ 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                      |          |      |      |    |
| (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 | 1.91 | 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                            |          |      |      |    |
| (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 inter-correlations: 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 Δ AICC < 3: Cover of litter

3Parameters that were excluded due to strong inter-correlations: 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 Δ AIC$_C$<3: Cover of rushes, cover of open soil, nectar abundance and sunshine duration

### 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 (Δ 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                      |          |      |      |    |
| (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                            |          |      |      |    |
| (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 Δ 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 inter-correlations: Vegetation height, vegetation density 25–30 cm height, cover of shrubs, cover of Poaceae, cover of rushes, cover of herbs, cover of mosses and cow pats (Appendix Table A1)

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

### Table 5

Mean values (± SE) of numerical parameters at oviposition 

| Parameter                        | Oviposition site | Random site | P       |
|----------------------------------|------------------|-------------|---------|
| Vegetation height (cm)³          | 13.8 ± 1.0       | 13.4 ± 1.8  | n.s.²   |
| Vegetation density (%)³          | 54.1 ± 6.0       | 50.0 ± 8.1  | n.s.³   |
| 10–15 cm height                 | 6.4 ± 2.1        | 4.3 ± 1.8   | n.s.³   |
| 25–30 cm height                 |                  |             |         |
| Cover (%) of Poaceae             | 34.8 ± 4.1       | 43.0 ± 7.0  | n.s.³   |
| Sedges                           | 30.4 ± 3.3       | 25.9 ± 3.2  | n.s.³   |
| Rushes                           | 6.6 ± 3.4        | 0.5 ± 0.5   | n.s.³   |
| Herbs                            | 19.6 ± 2.5       | 21.6 ± 6.9  | n.s.³   |
| Mosses                           | 95.7 ± 2.1       | 91.2 ± 5.6  | n.s.³   |
| Litter                           | 15.6 ± 4.1       | 15.7 ± 5.1  | n.s.³   |
| Sunshine duration (h)³           | 10.4 ± 0.2       | 11.0 ± 0.4  | n.s.³   |

³Measured three times at a randomly chosen location in the plot
²Measured within a frame of 30 cm depth and 50 cm width above ground (Poniatowski and Hartmann 2008)
³Measured for the month of August in the centre of the plot with a horizonoscope after Tonne (1954), accuracy ½ h
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; Akebono 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.
| 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                         |                    |                    |                  |                  |                 |                |               |                |                |                 |                 |                 |                          |
| Plot occupancy (Table 3a)         |                    |                    |                  |                  |                 |                |               |                |                |                 |                 |                 |                          |
| 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             | −            | −                        |
| 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***        | −0.37***       | 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                 | /                  |                    |                  |                 |                |                |               |                |                |                 |                 |                 | −              | −                        |
| Abundance (Table 3b)              |                    |                    |                  |                 |                |                |               |                |                |                 |                 |                 | −              | −                        |
| 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: 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 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    | Plot occupancy (Table 4a) |                    |                |                  |                |                |                |                |                    |                  |                    |                    |                     |
| 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                 | /                   | 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             |
| (10–15 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              |
| Density                 | /                   | −0.27              | −0.34*         | −0.43**          | −0.02          | 0.66***        | 0.12           | −0.35**         | −0.56***            | −0.28*           | −0.79***           | −0.19             |                     |
| 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             | −0.14            | 0.26             | −0.13            |                     |
| Cover of sedges                   | /                  | 0.32*              | −0.51***         | −0.10           | 0.02            | 0.38**         | 0.14          | 0.14           | 0.28*          | 0.21             | 0.21              | 0.37**           | 0.37**           |                     |
| Cover of rushes                   | /                  | −0.29*             | −0.44***         | −0.22           | 0.57***         | 0.43**         | 0.27*         | 0.40**         | −0.04          | 0.09             | −0.06             |                 |                 |                     |
| Cover of herbs                    | /                  | −0.11              | 0.04             | −0.12           | 0.21            | −0.10          | 0.21          | −0.10          | 0.09           | 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***        | 0.49***       | 0.49***        | 0.49***        | 0.49***          | 0.49***           | 0.49***          | 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 |
|-----------|---------------------|---------------------|-----------------|------------------|-----------------|----------------|--------------|---------------|----------------|------------------|------------------|------------------|----------------|----------------------|
| Abundance (Table 4b) | | | | | | | | | | | | | | |
| 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 |
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References

Akeboshi A, Takagi S, Murakami M, Hasegawa M, Miyashita T (2015) A forest-grassland boundary enhances patch quality for a grassland-dwelling butterfly as revealed by dispersal processes. J Insect Conserv 19:15–24. https://doi.org/10.1007/s10841-014-9732-7

Anthes N, Fartmann T, Hermann G, Kaule G (2003) Combining larval habitat quality and meta-population structure – the key for successful management of pre-Alpine Euphydryas aurinia colonies. J Insect Conserv 7:175–185. https://doi.org/10.1023/A:1012730422958

Barnosky AD, Matzke N, Chapin FS, Cox ME, Daffin GC, Helias MK, Holmoway T, Howard EA, Kucharik CJ, Monfreda C, Patzz JA, Prentice IC, Ramankutty N, Snyder PK (2005) Global consequences of land use. Science 309:570–574. https://doi.org/10.1126/science.1111772

Beb素质 A, Konvička M, Dvořák J, Fric Z, Havelda Z, Pavlíčko A, Vrábel V, Weidenhoffer Z (2002) Butterflies of the Czech Republic: species, behaviour and mode. In: Settele J, Konvička M, Shreeve T, van Dyck H (eds) Ecology of butterflies in Europe. Cambridge University Press, Cambridge, pp 29–42

German Meteorological Service (Deutscher Wetterdienst) (2020) Climate Data Center. https://cdc.dwd.de. Accessed 17 Nov 2020

Greub CE, Nakagawa S, Laws RJ, Jamien IG (2011) Multi-model inference in ecology and evolution: challenges and solutions. J Evol Biol 24:699–711. https://doi.org/10.1111/j.1420-9101.2010.02210.x

Halada L, Evans D, Romão C, Petersen J-E (2011) Which habitats of European importance depend on agricultural practices? Biodiv Conserv 20:2365–2378. https://doi.org/10.1007/s10531-011-9989-z

Helbing F, Blaeser TP, Löfler F, Fartmann T (2014) Response of Orthoptera communities to succession in alluvial pine woodlands. J Insect Conserv 18:215–224. https://doi.org/10.1007/s10841-014-9632-x

Henle K, Alard D, Clitherow J, Corb P, Fribank L, Kull T, McCracken D, Moritz RFA, Niemelä J, Rebane M, Wascher D, Watt A, Young J (2008) Identifying and managing the conflicts between agriculture and biodiversity conservation in Europe: a review. Agric Ecosyst Environ 124:60–71. https://doi.org/10.1016/j.agee.2007.09.005

Hermann G (2020) Miniois dryas (Scopoli, 1763) – Blaukernauge. In: Reinhardt R, Harpke A, Caspari S, Dolek M, Kühn E, Musche M, Trusch R, Wiemers M, Settele J (eds) Breitbartsatlas der Tagfalter und Wildschmetterlinge Deutschlands. Eugen Ulmer, Stuttgart, pp 342–343

Hothorn T, Bretz F, Westfall P (2008) Simultaneous inference in general parametric models. Biometrical J 50:346–365. https://doi.org/10.1002/bimj.200810425
IPBES (Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Service) (2019) Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. Bonn

Kalarus K, Nowicki P (2017) Resource use by the dryad butterfly is scale-dependent. Popul Ecol 59:179–187. https://doi.org/10.1007/s10144-017-0579-0

Kalarus K, Skórka P, Nowicki P (2013) Resource use in two contrasting habitat types raises different challenges for the dryad butterfly Minois dryas. J Insect Conserv 17:777–786. https://doi.org/10.1007/s10841-013-9560-1

Kleijn D, Kohler F, Baldi, A, Batary P, Concepcion E, Clough Y, Diaz M, Gabriel D, Holzschuch A, Knop E, Kovacs A, Marshall E, Tscharntke T, Verhulst J (2009) On the relationship between farmland biodiversity and land-use intensity in Europe. Proc Biol Sci 276:903–909. https://doi.org/10.1098/rspb.2008.1509

Krämer B, Poniatowski D, Fartmann T (2012) Effects of landscape and habitat quality on butterfly communities in pre-alpine calcareous grasslands. Biol Conserv 152:253–261. https://doi.org/10.1016/j.biocon.2012.03.038

Krause B, Culmsee H, Wesche K, Bergmeier E, Leuschner C (2011) Habitat loss of floodplain meadows in north Germany since the 1950s. Biodiv Conserv 20:2347–2364. https://doi.org/10.1007/s10531-011-9988-0

Lederbogen D, Rosenthal G, Scholle D, Trautner J, Zimmermann B, Kaule G (2004) Allmendweiden in Südbayern: Naturschutz durch landwirtschaftliche Nutzung. Angewandte Landschaftskol 62:1–469

Löffler F, Fartmann T (2017) Effects of landscape and habitat quality on Orthoptera assemblages in pre-alpine calcareous grasslands. Agric Ecosyst Environ 248:71–81. https://doi.org/10.1016/j.agee.2017.07.029

Marshall EJP, Brown VK, Boatman ND, Lutman PJW, Squire GR, Ward LK (2003) The role of weeds in supporting biological diversity within crop fields. Weed Res 43:77–89. https://doi.org/10.1017/S004369360300332x

Munguira ML, García-Barros E, Martín Cano J (2009) Butterfly herbivory and larval ecology. In: Settele J, Shreeve T, Konvička M, Van Dyck H (eds) Ecology of butterflies in Europe. CUP, Cambridge, pp 43–54

Nakagawa S, Johnson PCD, Schielzeth H (2017) The coefficient of determination R2 and intra-class correlation coefficients from general linear mixed-effects models revisited and expanded. J R Soc Interface 14:20170213. https://doi.org/10.1098/rsif.2017.0213

Nakagawa S, Schielzeth H (2013) A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods Ecol Evol 4:133–142. https://doi.org/10.1111/j.2041-8112.2012.00261.x

Oberdorfer E (1992) Süddeutsche Planzengesellschaften. Teil 1. Fels- undMauergesellschaften, alpine Fluren, Wasser-, Verlandungs- undMoosgesellschaften, 3rd edn. Gustav Fischer Verlag, Jena, Stuttgart, New York

Pollard E, Yates TJ (1993) Monitoring butterflies for ecology and conservation. Chapman and Hall, London

Poniatowski D, Fartmann T (2008) The classification of insect communities: lessons from Orthoptera assemblages of semi-dry calcareous grasslands in central Germany. Eur J Entomol 105:659–671. https://doi.org/10.1111/j.1439-0471.2008.01411.x

R Development Core Team (2018) R: a language and environment for statistical computing. http://www-r-project.org. Accessed 01 Jan 2018

Reinhardt R, Bolz R (2011) Rote Liste und Gesamtartenliste der Tagfalter (Rhopalocera) (Lepidoptera: Papilionoidea et Hesperioida) Deutschlands. In: Binot-Hafke M, Balzer S, Becker N, Gruttke H, Haupt H, Hofbauer N, Ludwig G, Matzeke-Hajek G, Strauch M (eds) Rote Liste gefährdeter Tiere, Pflanzen und Pilze Deutschlands. Band 3: Wirbellose Tiere (Teil 1). Naturschutz und Biologische Vielfalt 70(3):167–194

Rockström J, Steffen W, Noone K, Persson A, Chapin FS, Lambin EF, Lenton TM, Scheffer M, Folke C, Schellnhuber HJ, Nykvist B, de Wit CA, Hughes T, van der Leeuw S, Rodhe H, Sormin S, Snyder PK, Costanza R, Svedin U, Falkenmark M, Karlberg L, Corell RW, Fabry VJ, Hansen J, Walker B, Liverman D, Richardson K, Crutzen P, Foley JA (2009) A safe operating space for humanity. Nature 461(7263):472–475. https://doi.org/10.1038/nature08144

Sachtelen J, Winterholler M (2013) Blaukäurne Minois dryas. In: Braun M, Bolz R, Kolbeck H, Nummer A, Voith J, Wolf W (eds) Tagfalter in Bayern. Eugen Ulmer, Stuttgart

Sala OE, Chapin FS, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A, Lee-mans R, Lodge DM, Mooney HA, Oesterheld M, Poff NL, Sykes MT, Walker BH, Walker M, Wall DH (2000) Global biodiversity scenarios for the year 2100. Science 287:1770–1774. https://doi.org/10.1126/science.287.5459.1770

Schwarz C, Trautner J, Fartmann T (2018) Common pastures are important refuges for a declining passerine bird in a pre-alpine agricultural landscape. J Ornithol 159:945–954. https://doi.org/10.1007/s10336-018-1561-0

Settele J, Dover J, Dolek M, Konvička M (2009) Butterflies of European ecosystems: impact of land use and options for conservation management. In: Settele J, Shreeve T, Konvička M, Van Dyck H (eds) Ecology of butterflies in Europe. CUP, Cambridge, pp 353–370

Stoate C, Boatman ND, Borralho RJ, Carvalho CR, de Snoo GR, Eden P (2001) Ecological impacts of arable intensification in Europe. J Environ Manage 63:337–365. https://doi.org/10.1006/jema.2001.0473

Storkey J, Meyer S, Still KS, Leuschner C (2012) The impact of agricultural intensification and land-use change on the European arable flora. Proc Biol Sci 279:1421–1429. https://doi.org/10.1098/rspb.2011.1686

Streitberger M, Hermann G, Kraus W, Fartmann T (2012) Modern forest management and the decline of the Woodland Brown (Lopingia achine) in Central Europe. Forest Ecol Manag 269:239–248. https://doi.org/10.1016/j.foreco.2011.12.028

Stuhldreher G, Fartmann T (2014) When habitat management can be a bad thing – effects of habitat quality, isolation and climate on a declining grassland butterfly. J Insect Conserv 18:965–979. https://doi.org/10.1007/s10841-014-9704-y

Succow M, Jeschke L (1990) Moore in der Landschaft. Urania-Verlag, Leipzig

Thomas JA (2005) Monitoring change in the abundance and distribution of insects using butterflies and other indicator groups. Phil Trans R Soc Lond B Biol Sci 360:339–357. https://doi.org/10.1098/rstb.2004.1585

Thomas JA, Telfer MG, Roy DB, Preston CD, Woodward JS, Asher J, Fox R, Clarke RT, Lawton JH (2004) Comparative losses of British butterflies, birds, and plants and the global extinction crisis. Science 303:1879–1881. https://doi.org/10.1126/science.1095046

Tonne F (1954) Besser bauen mit Besonnungs- und Tageslicht-Pla-nung. Karl Hofmann, Schorndorf

van Swaay CAM, Warren MS (1999) Red Data Book of European Butterflies (Rhopalocera). Nature and Environment, No. 99. Council of European Publishing, Strasbourg

Veen P, Jefferson R, de Smidt J, van der Straaten J (2009) Grasslands in Europe of high nature value. KNNV Publishing, Zeist

Watt WB, Boggs CL (2003) Synthesis: butterflies as model systems in ecology and evolution – present and future. In: Boggs CL, Watt WB, Ehrlich PR (eds) Butterflies – ecology and evolution taking flight. The University of Chicago Press, Chicago, pp 603–613
Weidemann H-J (1995) Tagfalter: beobachten, bestimmen, 2nd edn. Naturbuch-Verlag, Augsburg
Weking S, Hermann G, Fartmann T (2013) Effects of mire type, land use and climate on a strong declining wetland butterfly. J Insect Conserv 17:1081–1091. https://doi.org/10.1007/s10841-013-9585-5
 Wiklund C (1984) Egg-laying patterns in butterflies in relation to their phenology and the visual apparency and abundance of their host plants. Oecologia 63:23–29. https://doi.org/10.1007/BF00379780
Wilson RJ, Roy DB (2009) Butterfly population structure and dynamics. In: Settele J, Shreeve T, Konvička M, Van Dyck H (eds) Ecology of butterflies in Europe. Cambridge University Press, Cambridge, pp 81–96

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