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Restoration of calcareous grasslands: The early successional stage promotes biodiversity

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ABSTRACT

Land-use change has been identified as the most important factor responsible for the recent loss of biodiversity. One major problem is the abandonment of management, especially in semi-natural grassland ecosystems. Numerous restoration projects were, therefore, launched to counteract this development. However, the effects of restoration are not yet fully understood. Especially the early successional stage, i.e. the composition of the vegetation in the first years after the restoration measures, has received little attention probably due to its supposedly low conservation value.

As study area, we selected the largest area of calcareous grasslands at the northern edge of the German uplands. About 35 ha of formerly abandoned calcareous grasslands have been restored by cutting shrubs here in the last eight years. Within the restored sites, 50 randomly chosen vegetation surveys were made and the results were compared to 50 control plots.

Our study revealed that the value of the early successional stage for biodiversity conservation was previously underestimated. Even though the target state – calcareous grassland – is far from being reached, the early successional stage enhances the conservation value of calcareous grasslands by (i) increasing diversity at the landscape scale, (ii) hosting numerous target species as well as (iii) contributing to a higher habitat quality and heterogeneity.

Future restoration of calcareous grasslands should focus on sites with low nutrient content of the soil, a shallow topsoil, and a warm microclimate. At such sites, the chances are greatest that species with a high nature conservation value, i.e. characteristic species of calcareous grasslands as well as thermophilous fringe and ruderal species, will re-establish.

1. Introduction

Land-use change has been identified as the most important factor responsible for the recent loss of biodiversity (Sala et al., 2000; Foley et al., 2005). The intensification of agricultural land-use, abandonment, afforestation and urbanisation have caused degradation, loss and fragmentation of semi-natural habitats, especially in temperate grassland ecosystems (Bakker and Berendse, 1999; WallisDeVries et al., 2002; Howard et al., 2003). Among them, calcareous grasslands have an outstanding value for nature conservation, due to their very diverse flora and fauna (Poschlod and WallisDeVries, 2002; van Swaay, 2002; Barbaro et al., 2004). As a result of the above-mentioned processes, species-rich calcareous grasslands have lost much of their original extent and become increasingly fragmented. Today, they are often situated in a matrix of intensively used agricultural land (Poniatowski et al., 2016, 2018b) which makes them a refuge for specialised species (Krämer et al., 2012; Poniatowski et al., 2018a; Löffler et al., 2019). Due to their role as biodiversity hotspots, and the great threats they face, they are priority habitats of the EU Habitats Directive.

Nevertheless, the habitat quality of calcareous grasslands has deteriorated in many places. In particular, the abandonment of traditional land-use causes problems (Poschlod et al., 2005; Galvánek and Lepš, 2008; Henle et al., 2008). Since low-intensity grazing on nutrient-poor sites is often no longer profitable, a few competitive grass and shrub species (e.g. *Brachypodium pinnatum*, *Prunus spinosa*) often become dominant (Kiehl, 2019). This changes light and soil conditions, which leads to a strong decline of species richness (Gazol et al., 2012; Neuenkamp et al., 2016). Numerous restoration projects were, therefore, launched to counteract this development. At the same time, this problem was scientifically addressed by ecologists who analysed

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experimentally which measures are suitable to restore abandoned calcareous grasslands (e.g. removal of a dense shrubbery and subsequent grazing). Most of these studies focused on measures that increase species richness. It has been shown that a low-intensity management leads to a significant increase in species numbers after a short period of just a few years (Bobbink and Willems, 1993; Zobel et al., 1996; Willems and Bik, 1998).

However, Mortimer et al. (1998) noted that the pure species numbers are not an optimal indicator for evaluating the success of restoration measures (see also Piqueray et al., 2011; Waldén and Lindborg, 2016). It seems better to check whether the previously defined target species have established. These might be characteristic species of calcareous grasslands and possibly other species with a high conservation value (cf. Kiehl and Pfadenhauer, 2007; Maccherini and Santi, 2012; Wagner et al., 2019). Additionally, the functional role of the plants should also be considered (Barbaro et al., 2001; Kollmann et al., 2016) – e.g. their importance for insects as pollen source or host plant. With regard to the latter aspect, the early successional stage, i.e. the composition of the vegetation in the first years after restoration measures like shrub cutting, may have a special significance for the conservation of biodiversity in calcareous grasslands (e.g. Thomas, 1993). Shortly after a restoration measure, the vegetation is usually characterised by a mixture of different ecological groups, especially pioneer and ruderal, but also some target species (Kiefer and Poschlod, 1996; Bisteau and Mahy, 2005; Dzwonko and Loster, 1998). However, this early successional stage has received little attention in restoration ecology so far, maybe because of its supposed low importance for nature conservation.

In the context of our large-scale study, we therefore, addressed the question if the value of the early successional stage is underestimated. To answer the question, we studied the number and cover of selected target species (typical species of calcareous grasslands, thermophilous fringes and ruderal habitats) and functional plant species (host plants and/or pollen sources for specialised insects) in areas where dense stands of shrubs had been cleared in order to restore the typical plant community of calcareous grasslands. It can be assumed that some pioneer and ruderal plant species, which are usually not in the focus of restoration measures, have a special significance for the promotion of biodiversity in calcareous grasslands. In particular, the following questions were addressed:

(i) Do target and functional plant species richness and cover differ between shrubs, restored grasslands and calcareous grasslands?
(ii) Are there indicator plant species characterising shrubs, restored grasslands or calcareous grasslands?
(iii) Which environmental factors determine richness and cover of the target species within the restored grasslands?

2. Material and methods

2.1. Study area

The study area is located at the northern edge of the German uplands. More specifically, it comprises the middle and lower part of the Diemel Valley along the border between the federal states of North Rhine-Westphalia and Hesse (51°32′N/9°00′E and 51°36′N/9°24′E) at an elevation of 160 to 280 m a.s.l. (Fig. 1). The climate is suboceanic with mean annual temperatures of 7.5–9 °C and a mean annual precipitation of 650–800 mm. Typical elements of the study area are calcareous grasslands (~400 ha), which lie isolated in an intensively used agricultural and forested landscape. As a part of the Diemel Valley, the study area belongs to the largest area of semi-dry calcareous grasslands in the northern half of Germany (Fartmann, 2004).

2.2. Subareas and plots

Within the study area, we investigated all calcareous grasslands where restoration measures had been carried out in a period of eight years prior to our study ($N_{\text{patches}} = 16$). The area of these calcareous grasslands varied between 1.7 and 20.5 ha (mean: 8.6 ha, total restored area: 35 ha). To avoid problems with spatial autocorrelation, we grouped closely adjacent calcareous grasslands to subareas (see also Section 2.5: LMM and GLMM with random effects). Altogether, ten subareas were defined (Fig. 1). Within these subareas, plant diversity was studied in 100 randomly selected plots. The number of plots per subarea depended on the size and the habitat configuration of the subarea and varied between six and 16 plots . In each subarea, three habitat types were differentiated:

(i) Calcareous grasslands completely overgrown with shrubs due to the abandonment of management (shrub, 25 plots)
(ii) Sites of type i where shrubs had been cut and resprouting woody plants had been suppressed by mulching prior to the study and which are subject to low-intensity grazing since then (restored grassland, 50 plots) (Fig. 2a and b)
(iii) Target state: Extant calcareous grasslands with a long continuous history of low-intensity grazing (calcareous grassland, 25 plots) (Fig. 2d)

All plots had an area of 16 m^2 (4 m × 4 m) and were installed permanently. For this purpose, we used magnets, which were fixed in each corner of the plot with tent pegs. With the assistance of a magnet detector, the plots were precisely retrieved at subsequent visits.

2.3. Plot characteristics

For each of the 100 plots, several parameters of horizontal vegetation structure were recorded: cover of total vegetation, trees, shrubs, field layer, cryptogams, bare soil, gravel and stones as well as litter. In addition, the heights of the field layer and of shrubs were ascertained.

Among abiotic plot characteristics, we measured aspect, slope and the thickness of the topsoil (using a metal rod with length marks). In combination with the latitude of the study area, aspect and slope of a plot were used for calculating the amount of direct incident radiation (in MJ $cm^{-2} \times yr^{-1}$) as an approximate measure of the local climate (McCune and Keon, 2002).

Moreover, we analysed soil characteristics. Samples comprised of the mineral soil after removal of the humus layer were taken with a shovel at a soil depth of 10 cm in August 2017 as mixed samples from three randomly chosen sub-samples per plot. Air-dried soil samples were sieved (2 mm mesh size) and prepared with calcium-acetate-lactate to measure soluble phosphorus (spectrophotometer) and potassium (flame photometer). Additionally, nitrate, ammonium, calcium and magnesium were analysed with an ion chromatograph. The soil reaction was measured using $CaCl_2$ solution (concentration: 0.01 mol/l).

The age of the restored plots, i.e. the time since shrub-cutting had been carried out, varied from three to eight years. However, this variable could not be used in the analyses because precise information on the date of the restoration measures was not available for all plots. Instead, we used the variables height of the shrub layer and total cover of vegetation as an indicator for the time period since the application of the restoration measures (Table A.1).

2.4. Plant sampling

Species richness and cover (%) of vascular plants were sampled three times per plot in spring and summer 2017. At the end of May we looked for early-flowering plants – especially some orchids. The main vegetation survey was conducted in mid-June. Later on, in the season (mid-August), we searched for late-flowering plants like gentian

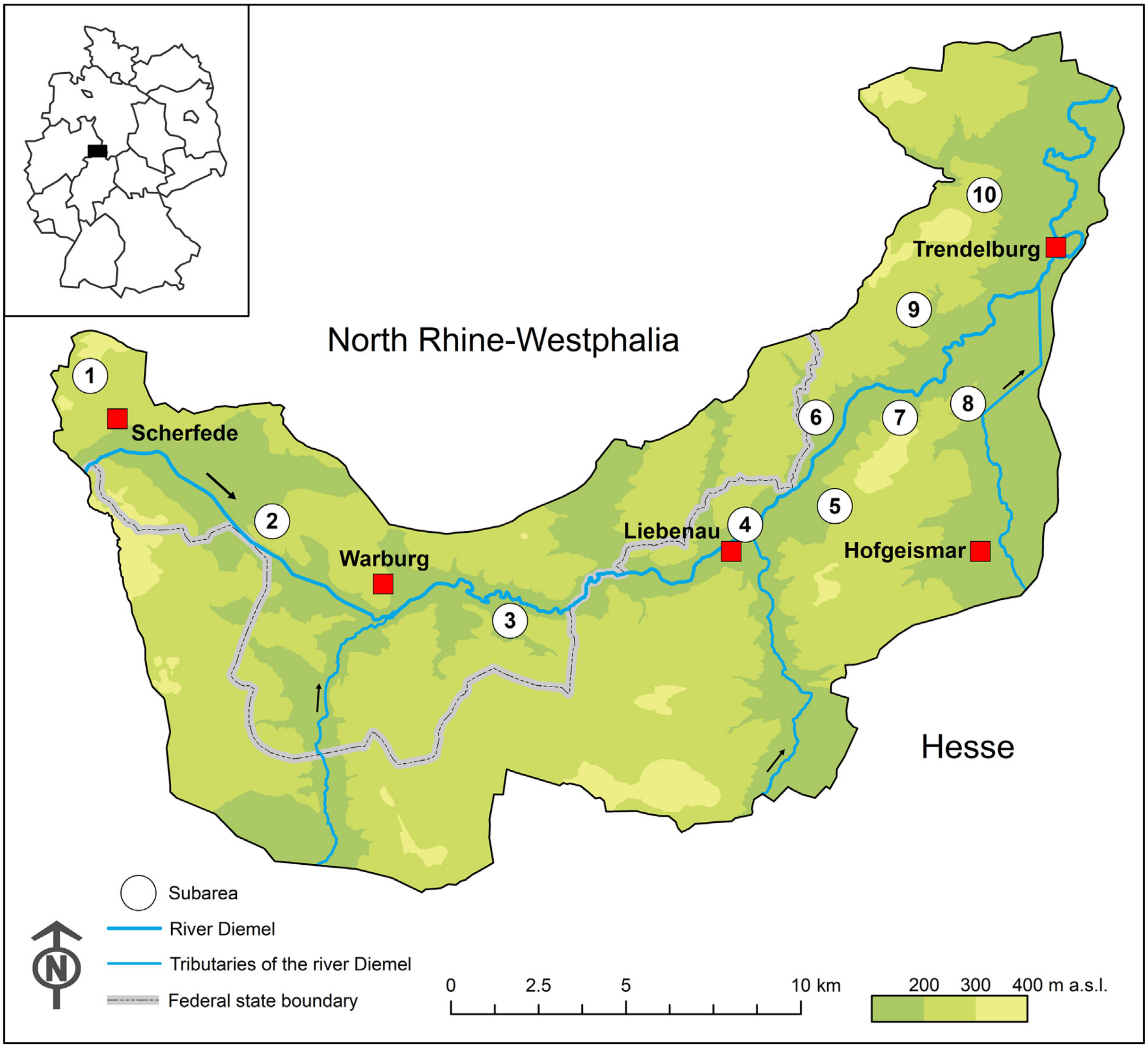

Fig. 1. The study area, the middle and lower Diemel Valley in central Germany (inlay), and the location of the ten subareas.

(*Gentianella* spp. and *Gentianopsis* spp.) and eyebright (*Euphrasia* spp.) species. Plants were classified into three ecological groups – all of which have a high nature conservation value (hereafter referred to as 'target species'): (i) characteristic species of calcareous grassland, (ii) thermophilous fringe species and (iii) thermophilous ruderal species. As reference, we used regional and national literature (Oberdorfer, 1993a, 1993b, 2001; Fartmann, 2004). Additionally, functional groups of species (hereafter referred to as 'functional species') were defined according to their importance as host plants and/or pollen sources for mono- and oligophagous planthoppers and butterflies as well as for mono- and oligolectic wild bees (Nickel, 2003; Fartmann, 2004; Westrich, 2018). The threat status of the plant species was taken from Hemm et al. (2008) and Raabe et al. (2010) (hereafter referred to as 'threatened species'). The nomenclature follows Buttler and Thieme (2018).

2.5. Statistical analysis

2.5.1. Comparison of habitat types

The environmental conditions at the three habitat types were compared via Kruskal-Wallis *H* test and Dunn's post-hoc test using SigmaPlot 14.0 (Systat Software, San Jose, CA, US). We chose this non-parametric approach because most of the environmental parameters had highly skewed distributions and, thus, could not be analysed via mixed-effects models as it was done in the case of species numbers and cover (see below).

In order to identify species that were highly characteristic either for shrubs, restored grasslands, or calcareous grasslands, Indicator Species Analysis (ISA; Dufrêne and Legendre, 1997) was carried out for all vegetation relevés by using PC-ORD 5.0 (MjM Software Design, Gleneden Beach, OR, US).

The number and cover of all, functional, target and threatened species were compared between shrubs, restored grasslands and calcareous grasslands by fitting mixed-effects models within the R environment (R-3.3.2; R Development Core Team) with *habitat type* as categorical predictor and *subarea* (see Section 2.2) as random intercept. Species number was modelled by Linear Mixed-effects Models (LMM) or Generalised Linear Mixed-effects Models (GLMM) with Poisson error structure using the lme4 package (Bates et al., 2015), depending on the distribution of the response variable. Species cover was modelled by GLMM with binomial error structure and Laplace Approximation for parameter estimation. As some of the binomial models showed over-dispersion, we routinely set up an observation-level random intercept nested in *subarea* in all of the GLMM. All-pairwise comparisons between habitat types were made using the function 'glht()' in the multcomp package (Hothorn et al., 2008) and the default 'single-step' method to

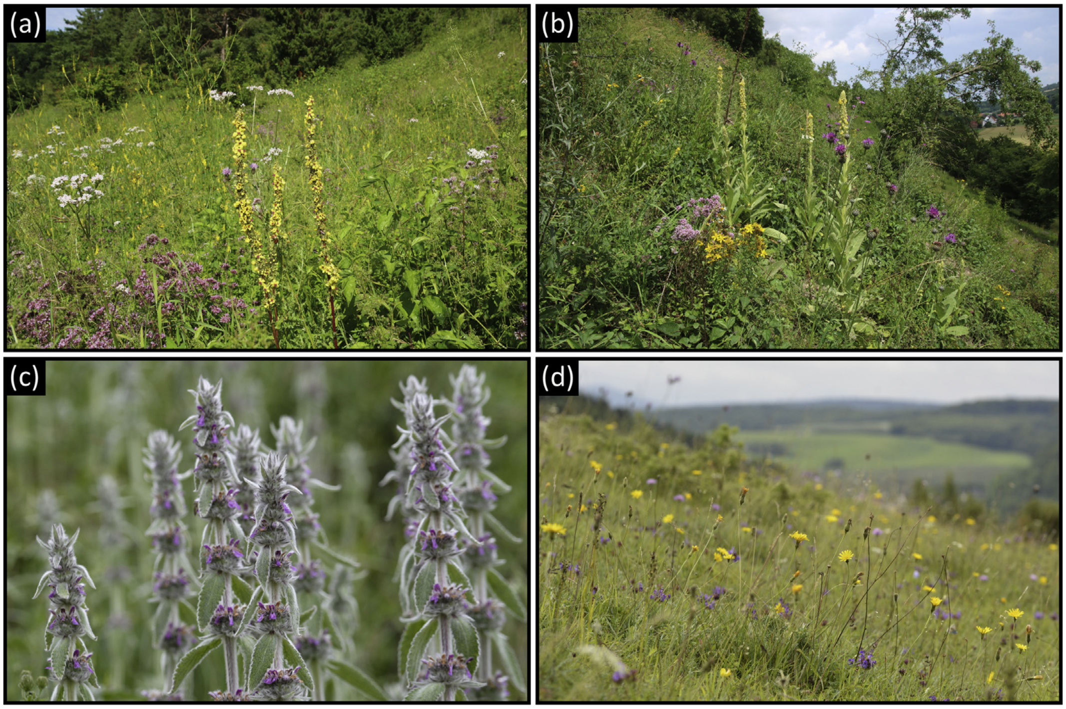

Fig. 2. Impressions of the vegetation surveys: a – flower-rich restored grassland at the foot of a slope with e.g. *Centaurea jacea*, *Melilotus altissimus*, *Origanum vulgare*, *Valeriana officinalis* agg. and *Verbascum nigrum* (Photo: D. Poniatowski); b – sun-exposed restored grassland at a steep slope with e.g. *Agrimonia eupatoria*, *Centaurea scabiosa*, *Hypericum perforatum*, *Origanum vulgare* and *Verbascum thapsus* (Photo: D. Poniatowski); c – *Stachys germanica* – a rare, thermophilous ruderal species, whose occurrence is restricted to sites where shrub-cutting has taken place (Photo: T. Fartmann); d – species-rich calcareous grassland with typical plants like *Brachypodium pinnatum*, *Briza media*, *Koeleria pyramidata*, *Leontodon hispidus*, *Prunella grandiflora* and *Scabiosa columbaria* (Photo: T. Fartmann).

adjust the *p* values for multiple testing.

2.5.2. Relationships between target species within the restored grasslands and environmental conditions

In order to analyse which environmental parameters (Table A.1) explained species richness and cover of the target species (see Section 2.4) within the restored grasslands, we fitted LMM and binomial GLMM, respectively, with the same random effects structure as described above. To avoid model overfitting, the analysis was performed in two steps: First of all, single-predictor (G)LMM were fitted for all combinations of response and predictor variables in order to detect which predictor variables had an impact on the response variable (Likelihood Ratio Tests, $P < .05$). In a second step, the global multiple-predictor models were calculated with the previously determined predictor variables. Out of the strongly intercorrelated variables *cover of bare ground and stones* and *cover of total vegetation* (Pearson correlation coefficient [r_p] = −0.84), only the latter was included in the models (cf. Dormann et al., 2013). To increase model robustness and to identify the most important environmental parameters, we applied model averaging based on an information-theoretic approach (Grueber et al., 2011). Model averaging was conducted using the ‘dredge’ function (R package MuMIn, Bartón, 2017) and only included top-ranked models within $\Delta AIC_C < 3$ (cf. Grueber et al., 2011).

3. Results

3.1. Environmental conditions

The majority of the environmental parameters significantly differed between the three habitat types (Table 1). Differences were most pronounced between shrubs on the one hand and the two grassland types on the other hand. However, in some cases restored grasslands had an intermediate position between shrubs and calcareous grasslands. In contrast to grassland plots, shrub plots were characterised by a well-established (tall, high cover) shrub layer, a high litter cover and low field layer cover. Additionally, soil pH values were lower, and contents of phosphate and potassium were higher at shrubs.

Restored grasslands had the deepest soil and tallest field layer, both decreasing from restored grasslands over shrubs to calcareous grasslands. Shrubs and restored grasslands had the lowest cover of mosses and the highest contents of ammonium/nitrate in the soil (N_{min}) in common. All other environmental parameters did not differ between the three habitat types or at least pairwise comparisons did not reveal any differences.

3.2. Plant species assemblages

In total, we found 297 taxa of vascular plants on the 100 plots; among them were 50 (17%) threatened species. Overall species richness was highest in restored grasslands and calcareous grasslands with an average of 45 and 42 species per plot, respectively, significantly differing from shrubs (Fig. 3a). The number of threatened species significantly increased from shrubs over restored grasslands to calcareous grasslands (Fig. 3b).

The ISA identified for all habitat types a variety of plant indicator species (Table A.2): 15 species were determined as indicators for shrubs. Most of them were shrub, woodland or nitrophilous ruderal species. Restored grasslands were characterised by 34 indicator species belonging to several ecological groups such as species of shrubberies, mesic grasslands, clear-cuts, thermophilous fringes as well as thermophilous and nitrophilous ruderal habitats. With 50 species, most indicator species were identified for the calcareous grasslands. The composition of these grasslands was much more homogenous than those of the restored grasslands as it exclusively consisted of typical grassland species.

The pattern of the calcareous grassland species was similar to that of the threatened species (Fig. 4a and b): both species richness and cover significantly increased from shrubs over restored grasslands to

Table 1
Mean values (± SE) of environmental parameters in the three habitat types. Differences between the habitat types were tested using Kruskal-Wallis *H* tests and Dunn's post-hoc tests (for details see Section 2.5).

Parameter	Shrub	Restored grassland	Calcareous grassland	*P*
Local climate				
Direct incident radiation[1]	0.83 ± 0.02	0.83 ± 0.02	0.83 ± 0.02	n.s.
Vertical habitat structure (cm)				
Field layer	21.1 ± 2.4^a	31.4 ± 1.7^b	10.4 ± 1.3^c	***
Shrub layer	372.0 ± 24.7^a	58.7 ± 7.8^b	21.0 ± 13.9^c	***
Horizontal habitat structure (%)				
Total vegetation	91.1 ± 1.7	85.5 ± 1.7	91.8 ± 1.5	*
Tree layer	20.6 ± 6.5	2.0 ± 1.6	0.0 ± 0.0	***
Shrub layer	74.2 ± 4.6^a	8.8 ± 1.6^b	0.4 ± 0.2^c	***
Field layer	34.0 ± 6.0^a	78.7 ± 2.4^b	87.5 ± 1.8^b	***
Moss layer	17.2 ± 5.8^a	6.6 ± 1.7^a	43.6 ± 6.1^b	***
Bare ground	12.6 ± 2.7	8.1 ± 1.3	4.5 ± 1.0	n.s.
Gravel/stones	1.3 ± 0.6	2.3 ± 0.5	1.0 ± 0.3	n.s.
Litter layer	54.8 ± 6.2^a	22.3 ± 2.8^b	19.4 ± 2.9^b	***
Soil properties				
pH	7.0 ± 0.3^a	7.3 ± 0.04^{ab}	7.4 ± 0.03^b	**
Depth of the topsoil (cm)	21.3 ± 1.4^{ab}	25.1 ± 1.5^a	18.7 ± 1.5^b	*
Ion content (mg/100 g soil)				
Potassium	23.7 ± 4.1^a	13.3 ± 1.5^{ab}	8.5 ± 1.2^b	**
Calcium + Magnesium	15.7 ± 1.0	17.4 ± 0.6	15.7 ± 0.7	n.s.
Phosphate	0.7 ± 0.1^a	0.3 ± 0.02^b	0.3 ± 0.02^b	***
Ammonium + Nitrate (N_{min})	13.1 ± 1.9^a	9.0 ± 1.1^a	2.5 ± 0.5^b	***

n.s. = not significant. Different letters indicate significant differences ($P < .05$).
[1] Direct incident radiation was calculated according to McCune and Keon (2002) (s. Section 2.3).
* $P < .05$.
** $P < .01$.
*** $P < .001$.

calcareous grasslands. In contrast, the number and cover of thermophilous fringe and thermophilous ruderal species significantly peaked at restored grasslands (Fig. 4c–f).

Although diet-specialised planthoppers use other host plants than mono- or oligophagous butterflies (less than 20% consistency), the pattern was similar for both insect groups: species number and cover of the host plants significantly increased from shrubs over restored grasslands to calcareous grasslands (Fig. 5a–d). In contrast, species number and cover of the pollen sources of specialised wild bees was significantly lowest at shrubs but did not differ between the two grassland types (Fig. 5e and f). However, the pollen-source composition strongly differed between the two grassland types (Table A.2). Characteristic pollen sources of the restored grasslands were for example *Taraxacum* sect. *Ruderalia*, *Cirsium arvense*, *Cirsium vulgare*, *Picris hieracioides*, *Inula conyzae*, *Daucus carota* and *Clinopodium vulgare*. By contrast, in calcareous grasslands *Lotus corniculatus*, *Scabiosa columbaria*, *Hieracium pilosella*, *Leontodon hispidus*, *Leucanthemum vulgare* agg. and *Achillea millefolium* were the most frequent indicator species that serve as pollen sources for wild bees.

3.3. Response of target species in restored grasslands to environmental conditions

The nutrient content was the parameter with the strongest effect on the target species (Table 2). The number and cover of calcareous grassland species as well as the cover of thermophilous fringe species decreased with increasing ammonium/nitrate content in the soil (N_{min}) (Table 2a, b and d). Additionally, the potassium content had a negative effect on the number of calcareous grassland species (Table 2a). For the cover of thermophilous fringe species, a high cover of the total vegetation and shallow soils were further predictors (Table 2d).

The response of the thermophilous ruderal species to the environmental conditions was completely different from those of the two other groups of target species (Table 2). The number of species decreased with the cover of the total vegetation and increased with the potassium content (Table 2e). A highly warm local climate (direct incident radiation) favoured the cover of thermophilous ruderal species (Table 2f).

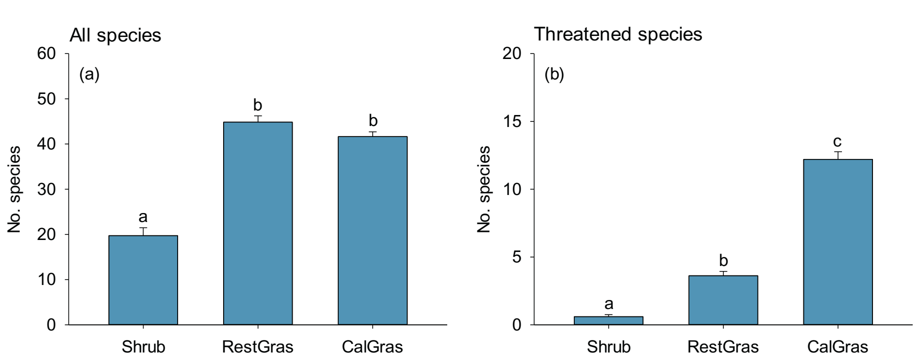

Fig. 3. Mean number (± SE) of all species (a) and threatened species (b) for the three habitat types (shrub [n = 25], restored grassland [RestGras; n = 50] and calcareous grassland [CalGras; n = 25]). Differences between the habitat types were tested using mixed-effects models with *subarea* as random intercept (for details see Section 2.5). Different letters indicate significant differences ($P < .05$).

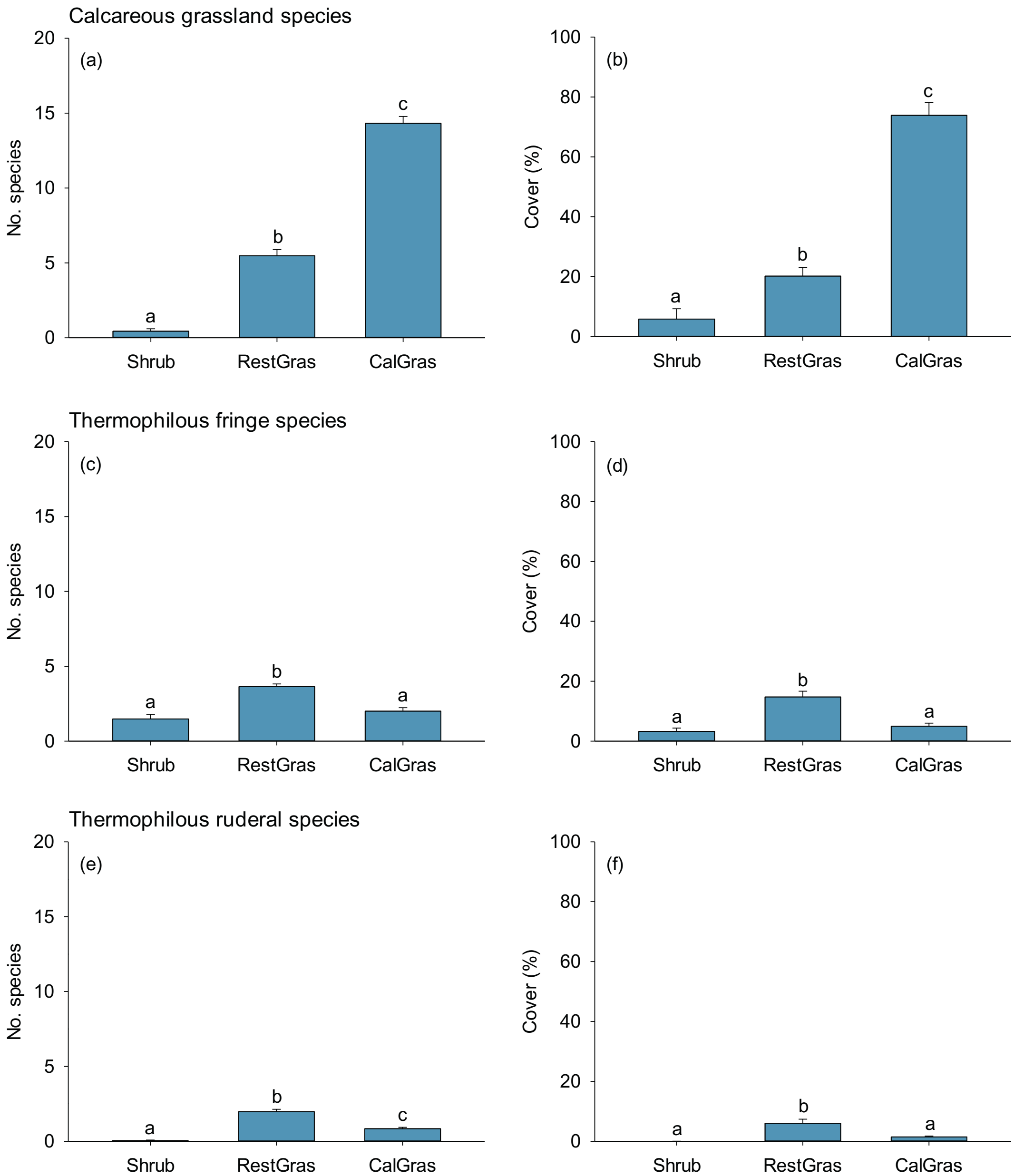

Fig. 4. Mean values (± SE) of number and cover of target species for the three habitat types (shrub [$n = 25$], restored grassland [RestGras; $n = 50$] and calcareous grassland [CalGras; $n = 25$]). (a) and (b): characteristic species of calcareous grasslands, (c) and (d): characteristic species of thermophilous fringes, (e) and (f): characteristic species of thermophilous ruderal habitats (for details see Section 2.4). Differences between the habitat types were tested using mixed-effects models with *subarea* as random intercept (for details see Section 2.5). Different letters indicate significant differences ($P < .05$).

4. Discussion

4.1. Differences between restored grasslands and target assemblages

This study showed that the restoration of degraded calcareous grasslands overgrown by shrubs through cutting of shrubs and mulching of resprouting woody plants has led to a significant increase in typical calcareous grassland species three to eight years after conducting the restoration measures. However, plant species composition of the restored grasslands still differed from those of the calcareous grasslands (target state). With regard to the characteristic calcareous grassland species, average species numbers were nearly three times and the cover almost four times higher in the calcareous grasslands than in the restored grasslands. For threatened species the results were similar. This indicates that the seed bank of degraded calcareous grasslands that were overgrown by dense shrubberies for many years or even decades are heavily impoverished. This is in line with the results of von Blanckenhagen and Poschlod (2005) showing that only about a quarter of the typical calcareous grassland species are able to build up a long-term persistent seed bank. Hence, the seed bank is of minor importance for the restoration of calcareous grasslands (Dutoit and Alard, 1995; Kalamees and Zobel, 1998; Bossuyt and Hermy, 2003; Bossuyt et al., 2006; but see Kalamees et al., 2012). Much more important is the re-colonisation by seed rain (Arruda et al., 2018). However, due to the limited dispersal ability of many calcareous grassland species (Mortimer et al., 1998; Bakker and Berendse, 1999; Poschlod et al., 1998), source populations in the immediate vicinity are necessary for a successful establishment of the plant assemblages (Dzwonko and Loster, 1998; Barbaro et al., 2001; Bisteau and Mahy, 2005).

Additionally, high nutrient levels in the topsoil of the restored sites often hamper the establishment of the target species (Bakker and Berendse, 1999; Kiehl, 2006; Moeslund et al., 2017; Kiehl, 2019). This

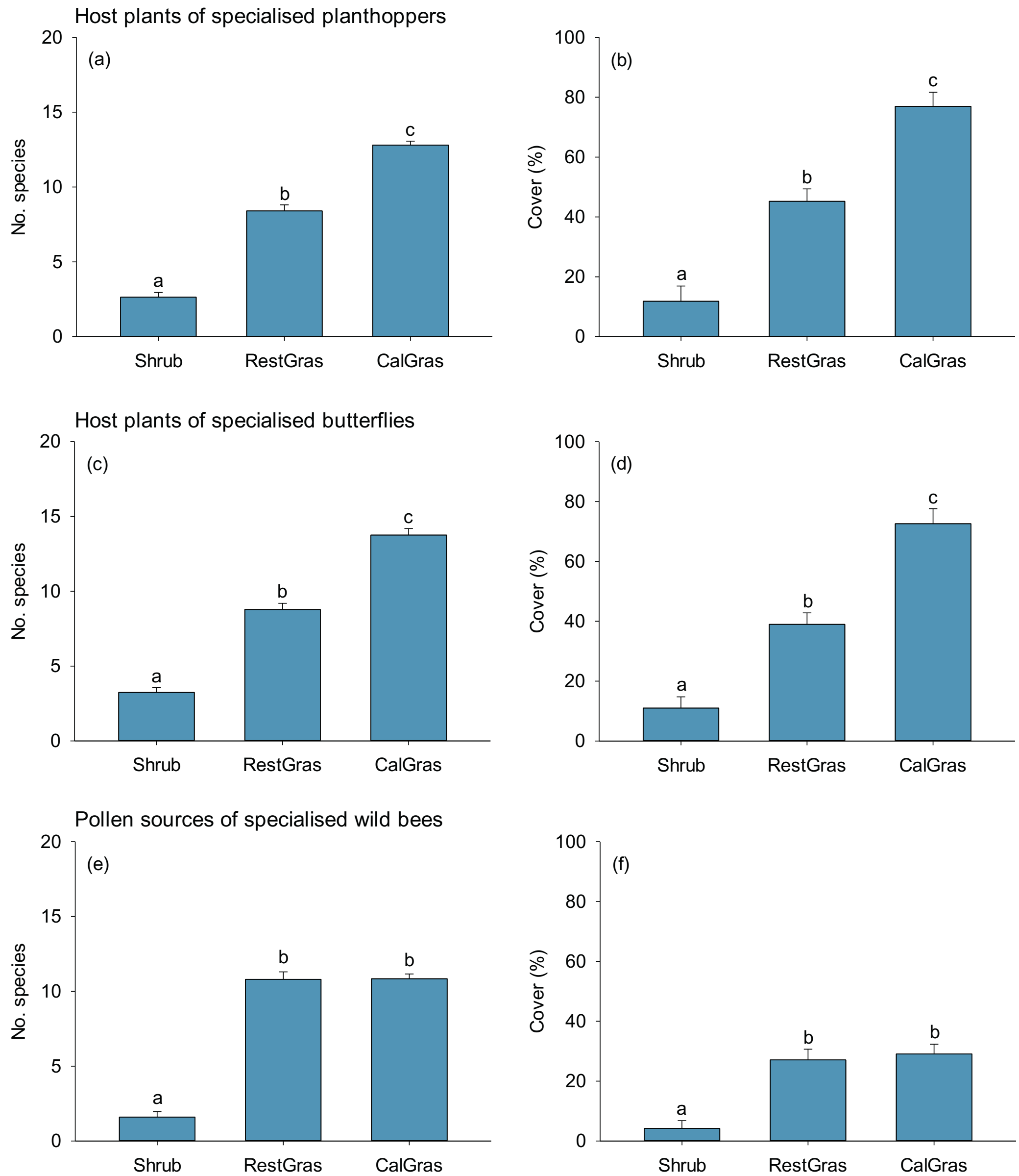

Fig. 5. Mean values (± SE) of number and cover of functional plant species for the three habitat types (shrub [n = 25], restored grassland [RestGras; n = 50] and calcareous grassland [CalGras; n = 25]). (a) and (b): host plants of specialised planthoppers, (c) and (d): host plants of specialised butterflies, (e) and (f): pollen sources of specialised wild bees (for details see Section 2.4). Differences between the habitat types were tested using mixed-effects models with *subarea* as random intercept (for details see Section 2.5). Different letters indicate significant differences ($P < .05$).

also applies to our sites. In calcareous grasslands overgrown by shrubs, the roots of the woody plants exploit nutrients from deeper soil layers, which are inaccessible to herbs or grasses and release them into the topsoil as mineralised leaf litter (Key, 1979). Therefore, we observed higher ammonium/nitrate contents in restored grasslands than in calcareous grasslands. High nutrient levels in the topsoil promote the establishment of nitrophilous ruderal and mesic grassland species, which are more competitive than the low-growing and light-demanding calcareous grassland species under these conditions (Kiefer and Poschlod, 1996; Bossuyt and Hermy, 2003; Jacquemyn et al., 2003). Additionally, they prevent the establishment of mycorrhiza, which in turn is vital for many calcareous grassland species (Hempel et al., 2013; Torrez et al., 2016; Moeslund et al., 2017). The negative effect of the high nutrient levels on the establishment of the calcareous grassland species is supported by our study. Within the restored grasslands, the number and cover of calcareous grassland species decreased with the ammonium/nitrate content. A regular management by grazing or mowing is, therefore, essential to reduce nutrients (Willems, 2001; Jacquemyn et al., 2003; Smits et al., 2008; Kiehl, 2019). However, the removal of nutrients and the interlinked establishment of typical calcareous grassland species is a time-consuming process. As a rule, it takes at least 10 years until the species composition of the restored sites has approached those of the target sites (von Blanckenhagen and Poschlod, 2005; Piqueray et al., 2011; Waldén and Lindborg, 2016).

4.2. The early successional stage promotes biodiversity

A mixture of species from different ecological groups is characteristic for the early successional stage after removal of shrubs (Kiefer and Poschlod, 1996; Bisteau and Mahy, 2005; Dzwonko and Loster, 1998; von Blanckenhagen and Poschlod, 2005). In addition to typical calcareous grassland species as well as thermophilous fringe and ruderal

Table 2
Global models: Influence of several environmental parameters (predictor variables) on the number and cover of the target species within the restored grasslands (n_{plots} = 50), analysed with Linear Mixed-effects Models (LMM) and Generalised Linear Mixed-effects Models (GLMM) (binomial error structure), respectively. (a) and (b): calcareous grassland species; (c) and (d): thermophilous fringe species; (e) and (f): thermophilous ruderal species (see also Table A.1). Model-averaged coefficients (conditional average) were derived from the top-ranked LMM/GLMM ($\Delta AIC_C < 3$).

Parameter	Estimate	SE	Z	*P*	Parameter	Estimate	SE	Z	*P*
Calcareous grassland species									
(a) No. of species					(b) Cover				
(Intercept)	8.05	0.818	9.6	***	(Intercept)	−1.16	0.318	−3.6	***
Ammonium + Nitrate	−0.14	0.048	−2.8	**	Ammonium + Nitrate	−0.09	0.028	−3.4	**
Potassium	−0.09	0.035	−2.5	*					
Height of shrubs	−0.01	0.007	−1.8	n.s.					
Thermophilous fringe species									
(c) No. of species					(d) Cover				
(Intercept)	−1.85	4.697	−0.4	n.s.	(Intercept)	−4.47	0.868	−5.0	***
Ammonium + Nitrate	−0.04	0.022	−1.9	n.s.	Ammonium + Nitrate	−0.08	0.016	−4.8	***
pH	1.05	0.537	1.9	n.s.	Cover of total vegetation	0.05	0.011	4.3	***
Phosphate	2.25	1.245	1.8	n.s.	Depth of the topsoil	−0.04	0.012	−3.2	**
Thermophilous ruderal species									
(e) No. of species					(f) Cover				
(Intercept)	4.01	1.409	2.8	**	(Intercept)	−6.23	1.893	−3.2	**
Cover of total vegetation	−0.03	0.012	−2.9	**	Direct incident radiation	4.25	1.714	2.4	*
Potassium	0.04	0.013	2.8	**	Height of shrubs	−0.01	0.003	1.8	n.s.
Depth of the topsoil	−0.02	0.013	−1.5	n.s.	Cover of total vegetation	−0.02	0.015	1.2	n.s.
Direct incident radiation	1.66	1.162	1.4	n.s.					

Statistical significances are indicated as follows: ****P* < .001, ***P* < .01, **P* < .05, n.s. = not significant.

species, numerous species of woodlands, shrubs, clear-cuts, mesic grasslands and nitrophilous ruderal habitats occurred in the restored grasslands (Table A.2). The target state – calcareous grassland – is, therefore, far from being reached (Section 4.1). However, we argue that the early successional stage clearly enhances both the taxonomic and the structural diversity of calcareous grasslands and, thus, their value for biodiversity conservation. As we outline in the following it increases (i) diversity at the landscape scale (gamma diversity), (ii) hosts numerous target species and (iii) contributes to a higher habitat quality and heterogeneity of the calcareous grasslands.

The restored grasslands were as diverse as the calcareous grasslands, but species composition clearly differed (cf. Bisteau and Mahy, 2005). Both types of grassland harboured a multitude of indicator species. Consequently, the restored grasslands contribute to a higher plant species diversity at the landscape scale. This in turn is likely to have positive effects on insect diversity, which usually increases with phytodiversity (Castagneyrol and Jactel, 2012).

As target species, we defined not only characteristic species of calcareous grasslands but also two groups of species with a high nature conservation value (i.e. thermophilous fringe and ruderal species). Our study proved that the latter two groups benefit greatly from the restoration measures. Their mean species number was significantly higher in restored grasslands than in the two other habitat types. In comparison to calcareous grassland species, thermophilous fringe and ruderal species are able to establish more rapidly as most of them have a persistent seed bank or a higher dispersal ability (cf. Dutoit and Alard, 1995; Kiefer and Poschlod, 1996; Poschlod et al., 1998). Particularly noteworthy in this context is the thermophilous ruderal species *Stachys germanica* (Fig. 2c). It is considered as threatened in Germany (Metzing et al., 2018) and occurred exclusively within the restored grasslands (indicator species, Table A.2).

Habitat quality is one or often even the most important factor determining the occurrence of specialised insect species (Thomas et al., 2011; Poniatowski et al., 2018b). It includes the vegetation structure of a habitat and the associated microclimate. Additionally, the cover of the host plants or pollen sources usually has a strong effect on patch occupancy (Franzén et al., 2009; Poniatowski et al., 2018b; Münsch et al., 2019). In our case, the restored grasslands harboured numerous pollen sources of mono- and oligolectic wild bees that did not occur in the calcareous grasslands and which are likely to benefit the local wild bee fauna.

The vegetation of the restored grasslands was taller than that of the calcareous grasslands. At the patch level, the restored grasslands, thus, contribute to a higher structural diversity (habitat heterogeneity) (Dzwonko and Loster, 1998; Bąba, 2003). A high structural diversity has generally a positive effect on the fauna, since hereby various types of microhabitats are available (Fartmann et al., 2012; Helbing et al., 2017; Löffler and Fartmann, 2017). Moreover, the high-growing vegetation of the restored grasslands may act as a microclimatic buffer by offering alternative habitat structures to drought-sensitive species that have to migrate into cooler and more humid microhabitats as a result of climate change (Fartmann, 2006; Streitberger et al., 2016).

5. Conclusions

The mechanical removal of dense shrubberies, which plays an important role in the restoration of calcareous grasslands, sets the vegetation back to an early successional stage, and the cleared sites can then be colonised by light-demanding grasses and herbs. In the restored grasslands that we studied, some typical species of calcareous grasslands have established within few years since the shrubs were removed, but in general the species composition was still clearly different from the target state. However, our results suggest that the plant assemblages of recently cleared formerly overgrown calcareous grasslands should not be regarded as a transitional stage of low-conservation value on the way to the re-establishment of calcareous grasslands. On the contrary, they should be viewed as an element that increases the structural and floristic diversity of the calcareous grasslands because they usually are very diverse mixtures of species from many different ecological groups.

Sometimes, the restored grasslands even harbour threatened species that occur neither in calcareous grassland nor in dense shrubberies, as it was the case with *Stachys germanica* in our study. Moreover, they provide a rich set of pollen sources that is substantially different from that of calcareous grasslands and, thereby, broaden the spectrum of food resources available to mono- and oligolectic wild bees.

Our study showed that the species richness of restored grasslands is subject to considerable variability which is related to soil properties (especially nutrient contents) and microclimate, but probably also other factors such as the composition of the seed bank and the vegetation in the vicinity of the restored grasslands. As a low nutrient content, a shallow topsoil and a warm microclimate favoured the establishment of the target species (typical species of calcareous grasslands, thermophilous fringes and thermophilous ruderal habitats) after shrub removal, we recommend that sites with these characteristics should be given priority in the planning of restoration measures.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecoleng.2020.105858.

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Supplementary data (Appendix A)

Table A1 Overview of the parameters recorded on the plots (n = 100) and the types of statistical analyses in which they were used. DCA = Detrended Correspondence Analysis, GLMM = Generalized Linear Mixed-effects Model, ISA = Indicator Species Analysis, LMM = Linear Mixed-effects Model (for details see Section 2.5).

Parameter	Scale level	Statistics
Response variables[1]		
No. species	metric	LMM, GLMM
Cover	metric	DCA[2], GLMM, ISA[3]
Predictor variables		
Local climate		
Direct incident radiation[4] (MJ cm^{-2} * yr^{-1})	metric	LMM, GLMM
Soil parameters		
pH	metric	LMM, GLMM
Depth of the topsoil (cm)	metric	LMM, GLMM
Ion content (mg/100g soil)		
Potassium	metric	LMM, GLMM
Calcium + Magnesium	metric	LMM, GLMM
Phosphate	metric	LMM, GLMM
Ammonium + Nitrate (Nmin)	metric	LMM, GLMM
Indicators for time since restoration		
Height of shrub layer (cm)	metric	LMM, GLMM
Cover of total vegetation (%)[5]	metric	LMM, GLMM

[1] Eight response variables: all species, threatened species, characteristic species of calcareous grasslands, thermophilous fringes and thermophilous ruderal sites as well as host plants of specialized planthoppers, host plants of specialized butterflies and pollen sources of specialized wild bees (for details see Section 2.4)

[2] DCA was only applied for the pollen sources ($n_{species}$ = 70) of the restored sites and the calcareous grasslands (for details see Section 2.5)

[3] Density of all species was used for ISA (for details see Section 2.5)

[4] Direct incident radiation was calculated according to McCune and Keon (2002) (s. Section 2.3)

[5] Cover of total vegetation was intercorrelated with cover of bare ground and stones (r_p = –0.84, P < 0.001)

Table A2 Indicator species of vascular plants for the three habitat types (results of ISA, Dufrêne and Legendre, 1997). IV = indicator value, ab = relative abundance comparing all habitat types, % = frequency. Grey shaded values: Species are indicator species for this habitat type. ***P < 0.001, **P < 0.01, *P < 0.05. Species were differentiated into nine ecological groups (Group) (Oberdorfer 1993a, b, 2001; Fartmann, 2004): Woodland species (wo), shrub species (sh), nitrophilous ruderal species (nr), grassland species (g) and species of clear-cuttings (cc) as well as (regional) characteristic species of thermophilous fringes (tf), thermophilous ruderal habitats (tr), mesic grasslands (mg) and calcareous grasslands (cg). Additionally, host plants (Host) for mono- and oligophagous planthoppers (Ph) and butterflies (Bf) as well as pollen sources for mono- and oligolectic wild bees were diffentiated (Nickel, 2003; Fartmann, 2004; Westrich, 2018).

Species	**Group**	**Host**		**PS**	***P***	**Shrub**			**Restored grassland**			**Calcareous grassland**		
		Ph	Bf			IV	ab	%	IV	ab	%	IV	ab	%
Prunus spinosa	sh	x	x	.	***	**71**	77	92	.	21	92	.	2	68
Crataegus spp.	sh	.	.	.	**	**63**	88	72	.	9	72	.	3	72
Fraxinus excelsior	wo	.	.	.	***	**55**	91	60	.	8	38	.	0	4
Geranium robertianum	nr/wo	.	.	.	***	**47**	90	52	.	10	18	.	0	0
Galium aparine	nr/wo	.	.	.	**	**47**	78	60	.	22	46	.	0	0
Cornus sanguinea	sh	.	.	.	*	**41**	60	68	.	39	76	.	1	28
Acer campestre	wo	.	.	.	**	**32**	73	44	.	27	28	.	0	0
Alliaria petiolata	nr	.	.	.	***	**28**	100	28	.	0	0	.	0	0
Dactylis polygama	wo	x	.	.	***	**26**	91	28	.	9	4	.	0	0
Galium odoratum	wo	.	.	.	**	**25**	88	28	.	12	12	.	0	0
Viola reichenbachiana	wo	.	x	.	*	**25**	61	40	.	39	16	.	0	0
Chaerophyllum temulum	nr	.	.	x	*	**21**	88	24	.	12	14	.	0	0
Sambucus nigra	sh	.	.	.	*	**17**	85	20	.	15	10	.	0	0
Moehringia trinervia	cc/nr/wo	.	.	.	**	**16**	97	16	.	3	2	.	0	0
Carex muricata agg.	cc	.	.	.	*	**15**	96	16	.	4	10	.	0	0
Taraxacum sect. *Ruderalia*	mg	.	.	x	***	.	3	20	**83**	97	86	.	1	16
Cirsium arvense	nr	.	.	x	***	.	0	0	**74**	100	74	.	0	0
Dactylis glomerata	mg	x	.	.	***	.	3	8	**71**	94	76	.	3	20
Galium mollugo agg.	mg	.	.	.	***	.	4	12	**69**	86	80	.	10	36
Hypericum perforatum	tf	.	.	.	***	.	4	12	**67**	81	82	.	15	40
Cirsium vulgare	nr	.	.	x	***	.	0	0	**56**	99	57	.	1	4
Picris hieracioides	tr	.	.	x	***	.	0	0	**56**	96	58	.	4	4
Rosa canina	sh	.	.	.	**	.	37	48	**56**	56	100	.	6	52
Rhamnus cathartica	sh	.	x	.	***	.	23	36	**55**	74	74	.	3	20
Fragaria vesca	cc	.	.	.	***	.	24	40	**51**	75	68	.	1	8
Rubus caesius	nr/wo	x	.	.	***	.	22	28	**50**	78	64	.	0	4
Sonchus asper	nr	.	.	.	***	.	0	0	**50**	100	51	.	0	0
Inula conyzae	tf	.	.	x	***	.	3	20	**49**	94	52	.	3	8
Viola hirta	tf	.	x	.	**	.	15	60	**49**	53	92	.	32	76
Daucus carota	tr	.	x	x	**	.	1	4	**48**	65	74	.	35	80
Clinopodium vulgare	tf	.	.	x	***	.	4	8	**47**	94	50	.	2	12
Clematis vitalba	sh	.	.	.	**	.	19	24	**45**	81	56	.	0	0
Origanum vulgare	tf	.	.	.	**	.	12	20	**39**	73	54	.	15	24
Geum urbanum	nr/sh/wo	.	.	.	*	.	51	60	**37**	49	76	.	0	0
Arrhenatherum elatius	mg	x	.	.	**	.	22	4	**34**	72	48	.	7	8

Table A2 Continued

Species	Group	Host		PS	*P*	Shrub			Restored grassland			Calcareous grassland		
		Ph	Bf			IV	ab	%	IV	ab	%	IV	ab	%
Poa angustifolia	g	x	.	.	**	.	19	12	**34**	74	46	.	8	12
Medicago lupulina	g	.	.	x	*	.	2	8	**34**	52	66	.	46	60
Trisetum flavescens	mg	.	.	.	*	.	9	12	**31**	58	54	.	33	32
Rubus idaeus	cc/nr/wo	x	.	.	**	.	0	0	**30**	100	30	.	0	0
Stachys germanica	tr	.	.	x	**	.	0	0	**26**	100	26	.	0	0
Geranium columbinum	nr	.	.	.	**	.	0	0	**24**	99	24	.	1	4
Cynoglossum officinale	tr	.	.	.	**	.	0	0	**22**	100	22	.	0	0
Bryonia dioica	nr	.	.	x	**	.	11	4	**21**	89	24	.	0	0
Atropa bella-donna	cc	.	.	.	**	.	0	0	**18**	100	18	.	0	0
Astragalus glycyphyllos	tf	.	.	.	*	.	1	4	**18**	98	18	.	1	4
Galeopsis tetrahit	cc/nr	.	.	.	*	.	2	4	**18**	98	18	.	0	0
Holcus lanatus	mg	x	x	.	*	.	0	0	**17**	97	18	.	3	4
Senecio erucifolius	tr	.	.	x	*	.	0	0	**16**	97	16	.	3	4
Carduus crispus	nr	.	.	x	*	.	7	4	**15**	93	16	.	0	0
Briza media	g	x	.	.	***	.	0	0	.	2	8	**98**	98	100
Cirsium acaule	cg	x	.	.	***	.	0	4	.	1	16	**95**	99	96
Lotus corniculatus	mg	x	x	x	***	.	0	4	.	12	35	**88**	88	100
Plantago media	g	.	x	.	***	.	0	0	.	4	10	**88**	96	92
Festuca ovina agg.	g	x	x	.	***	.	0	0	.	11	36	**86**	89	96
Scabiosa columbaria	cg	.	.	x	***	.	0	0	.	11	36	**79**	89	88
Hieracium pilosella	g	x	.	x	***	.	1	4	.	6	18	**78**	93	84
Sanguisorba minor	cg	.	x	.	***	.	0	8	.	21	64	**78**	78	100
Thymus pulegioides	g	x	x	.	***	.	0	0	.	8	22	**78**	92	84
Hippocrepis comosa	cg	x	x	x	***	.	0	0	.	5	24	**76**	95	80
Leontodon hispidus	mg	x	.	x	***	.	0	0	.	6	24	**75**	94	80
Koeleria pyramidata	cg	.	.	.	***	.	0	0	.	12	30	**74**	88	84
Potentilla neumanniana	cg	.	x	.	***	.	0	0	.	24	38	**73**	76	96
Plantago lanceolata	g	.	.	.	***	.	0	0	.	22	44	**72**	78	92
Linum catharticum	g	.	.	.	***	.	0	0	.	17	38	**70**	83	84
Carlina vulgaris	cg	x	x	.	***	.	0	0	.	5	18	**69**	95	72
Carex caryophyllea	cg	.	.	.	***	.	0	0	.	26	34	**68**	74	92
Helictotrichon pratense	cg	x	.	.	***	.	0	0	.	6	12	**68**	94	72
Pimpinella saxifraga	cg	.	x	.	***	.	5	8	.	19	48	**67**	76	88
Polygala comosa	cg	.	.	.	***	.	0	0	.	15	22	**64**	85	76
Brachypodium pinnatum	cg	x	x	.	***	.	12	20	.	30	68	**58**	58	100
Ranunculus bulbosus	cg	.	.	x	***	.	0	0	.	15	40	**58**	85	68
Galium pumilum	g	.	.	.	***	.	2	4	.	18	28	**51**	80	64
Euphrasia stricta	cg	.	.	.	***	.	0	0	.	1	2	**48**	99	48
Carex flacca	g	x	.	.	**	.	25	24	.	25	60	**46**	50	92
Leucanthemum vulgare agg.	mg	.	.	x	**	.	1	8	.	46	58	**42**	53	80
Achillea millefolium	mg	.	.	x	***	.	0	0	.	20	18	**41**	80	52
Gymnadenia conopsea	g	.	.	.	***	.	0	0	.	0	0	**40**	100	40
Ononis spinosa	cg	.	.	x	***	.	0	0	.	0	0	**40**	100	40
Galium verum	g	.	.	.	***	.	0	0	.	2	6	**39**	98	40

Table A2 Continued

Species	Group	Host		PS	*P*	Shrub			Restored grassland			Calcareous grassland		
		Ph	Bf			IV	ab	%	IV	ab	%	IV	ab	%
Knautia arvensis	mg	.	.	x	***	.	0	0	.	7	10	**33**	93	36
Centaurea scabiosa	cg	.	.	x	*	.	0	0	.	31	48	**33**	69	48
Prunella grandiflora	cg	.	.	.	***	.	0	0	.	0	0	**32**	100	32
Trifolium pratense	mg	.	x	x	**	.	0	4	.	21	26	**32**	79	40
Bromus erectus	cg	x	.	.	**	.	0	0	.	3	16	**31**	97	32
Genista tinctoria	g	.	x	.	***	.	0	0	.	0	0	**28**	100	28
Gentiana cruciata	g	.	x	.	***	.	0	0	.	0	0	**28**	100	28
Campanula glomerata	g	.	.	x	***	.	0	0	.	18	8	**26**	82	32
Campanula rotundifolia	g	.	.	x	**	.	0	0	.	32	12	**25**	68	36
Anthyllis vulneraria	cg	.	x	.	***	.	0	0	.	1	2	**24**	99	24
Prunella vulgaris	mg	.	.	.	*	.	3	8	.	31	24	**24**	65	36
Thymus praecox	cg	x	x	.	**	.	0	0	.	4	6	**23**	96	24
Orchis tridentata	g	.	.	.	***	.	0	0	.	0	0	**20**	100	20
Helianthemum obscurum	cg	x	x	.	**	.	0	0	.	8	4	**18**	92	20
Danthonia decumbens	g	.	.	.	*	.	0	0	.	5	4	**15**	95	16
Gentianella germanica	cg	.	.	.	*	.	0	0	.	3	2	**12**	97	12
Ononis repens	cg	.	.	x	*	.	0	0	.	0	0	**12**	100	12
Rhinanthus minor	mg	.	.	.	*	.	0	0	.	0	0	**12**	100	12
Trifolium montanum	g	.	.	x	*	.	0	0	.	0	0	**12**	100	12
Senecio jacobaea	mg	.	.	x	*	.	0	0	.	8	4	**11**	92	12