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Effects of different restoration treatments on long-term development of plant diversity and functional trait composition in calcareous grasslands

Auswirkung unterschiedlicher Renaturierungsverfahren auf die langfristige Entwicklung der pflanzlichen Artenvielfalt und der Pflanzenfunktionstypen in Kalkmagerrasen

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Abstract

Establishment of calcareous grassland on ex-arable fields by introducing target species is one of the most frequently used methods to restore the species assemblages of this highly endangered habitat type. The present study evaluates the long-term success of calcareous grassland restoration on former arable land in the vicinity of one of the oldest nature reserves in Bavaria, the "Garchinger Heide".

The restoration experiment combined different measures like topsoil removal, transfer of freshly cut seed-containing hay and additional sowing to the following variants in a 21-year experiment: (1) No topsoil removal, no hay transfer (control), (2) no topsoil removal with immediate hay transfer, (3) topsoil removal with immediate hay transfer and (4) topsoil removal with hay transfer 10 years after the start of restoration. Eleven Red List species which had not been transferred successfully were additionally sown after 9 to 19 years. Due to a limited availability of seeds, sowing of these species was mainly restricted to areas with topsoil removal, where better establishment was expected due to low vegetation cover. Five rare species with abundant seed production were also sown to plots without topsoil removal and hay transfer. The nature reserve served both as the donor area of the target species and as the reference to evaluate restoration success.

Regarding aboveground biomass and total vegetation cover, greatest similarity to the donor site was observed on plots without topsoil removal. In contrast, the highest numbers of target species occurred on plots with topsoil removal, hay transfer and additional sowing. Similarity in species composition between restoration sites and the reference area increased over time, but species composition of restored sites did not fully reflect the reference after 21 years. One reason for the remaining dissimilarity was probably that topsoil removal favored stress tolerant species which were less common on the mature and more fine-grained soils of the nature reserve. Plots without topsoil removal still differed from the reference by their high vegetation cover and a significantly higher proportion of mesophytic grassland species. The study also showed that 19 Red List species were successfully established on the former arable fields, eight of them presumably by sowing. Nevertheless, various other rare species have not

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been observed yet. Results on functional traits characterizing environmental adaptation and reproduction also underlined the differences between restoration plots and the reference site. Our study presents a 'dynamic restoration approach' where managers evaluated the original factorial treatments after a decade and modified them by additional treatments where development was sub-optimal. Such additional treatments may have confounded the experimental design, but from a management perspective proved to be a promising option to establish species rich grassland of high conservation value with a reasonable expenditure of time.

Keywords: dry grassland, ex-arable field, hay transfer, Red List species, sowing, species richness, topsoil removal

Erweiterte deutsche Zusammenfassung am Ende des Artikels

1. Introduction

Calcareous grasslands are among the most species-rich habitats in Europe and harbor high numbers of threatened plant and animal species (WILSON et al. 2012). During the 20th century, abandonment, afforestation, and conversion to productive grassland or arable fields led to a substantial loss and fragmentation of formerly large and connected grasslands (POSCHLOD & WALLISDEVRIES 2002, VEEN et al. 2009, DENGLER et al. 2014). As a consequence, remnants of calcareous grasslands are often too small and isolated to maintain viable populations of specialized plant species (FISCHER & STÖCKLIN 1997, WILLEMS 2001, KRAUSS et al. 2010). Therefore, conservation of calcareous grasslands became a key issue of the EU conservation policy (EUROPEAN COMMISSION 2007). Beyond the optimization of current management calcareous grassland can also be actively restored on sites formerly converted to productive grassland or arable fields in order to raise the amount of suitable habitats and to reduce fragmentation (FAGAN et al. 2008, TÖRÖK et al. 2011).

There are, however, two major constraints to a successful re-establishment (BAKKER & BERENDSE 1999): First, many species of calcareous grassland have a transient to short-term persistent seed bank and lack efficient dispersal strategies (HUTCHINGS & BOOTH 1996, MAURER et al. 2003, DIACON-BOLLI et al. 2013, CONRADI & KOLLMANN 2016). In addition, the lack of traditional dispersal processes like transhumance restricts the spread of propagules in present landscapes (WAGNER et al 2013, RICO et al. 2014). As a consequence, spontaneous colonization of restored sites from the seed bank and from remaining source patches frequently fails and active measures of species introduction and seed transfer are necessary to overcome dispersal barriers (KIEHL et al. 2010). The direct transfer of seed-containing green hay from suitable donor sites to restoration sites has several advantages: it includes large numbers of desired species, it preserves the regional gene pool, it is cheap and easily feasible, and the hay layer protects seedlings from desiccation (KIEHL et al. 2010, TÖRÖK et al. 2011). Furthermore, the high nutrient concentrations and large weed seed banks in ex-arable soils can last for decades and often reduce restoration success by favoring competitive arable weeds and ruderals (VERHAGEN et al. 2001). It has been proven that topsoil removal is an effective tool to remove both soils with high nutrient concentrations and the seed bank of competitive species (VERHAGEN et al. 2001, HÖLZEL & OTTE 2003, BAKKER et al. 2012).

The recovery of species-rich grasslands after disturbance is generally slow (WILLEMS 2001, HIRST et al. 2005) and it may take decades until conformity between re-established assemblages and the target community – i.e. the plant community of the donor site –

is achieved (Fagan et al. 2008). Therefore, long-term monitoring of re-established communities provides the most reliable information on the restoration success. However, even if restoration of other grassland types is considered, the availability of such studies is limited (Fagan et al. 2008, Heslinga & Grese 2010, Kiehl et al. 2010, Matthews & Spyreas 2010, Woodcock et al. 2011, Waldén & Lindberg 2016, Smith et al. 2017, Harvolk-Schöning et al. 2020). Here, we present results on the effects of different restoration measures on the establishment of calcareous grassland from 21 years of monitoring on restoration sites in the vicinity of the nature reserve Garchinger Heide, a calcareous grassland north of Munich, Germany. Due to its unique species composition with steppe, sub-mediterranean and alpine floristic elements (Windolf 1989), and its outstanding number of rare species, the 'Garchinger Heide' became one of the first nature reserves in Bavaria more than 100 years ago. It harbors 61 higher plant species included in the Red Lists of Germany (BfN 2018) and Bavaria (Scheuerer & Ahlmer 2003). As environmental change increasingly affected the species diversity of this old grassland (Bauer & Albrecht 2019), arable fields in the surrounding were bought to provide additional areas to preserve the typical flora and to encourage the threatened species (Pfadenhauer & Kiehl 2003). On these ex-arable fields, we tested the effects of different combinations of topsoil removal, hay transfer, and sowing of target species on plant species composition and diversity, and compared the results with vegetation data from the reference grasslands of the nature reserve. In addition, we studied the functional trait composition of restoration plots and reference grasslands in order to improve the mechanistic understanding of the effects of the restoration treatments. As functional traits reflect plant adaptation to the environment (Weiher et al. 1999, Westoby et al. 2002), they also provide a useful tool to understand which ecological filters act during community assembly (Kahmen et al. 2002, Pywell et al. 2003).

In detail we focused on the following questions: (1) How successful were the different treatments in establishing the target species of the nature reserve? (2) To what extent does species composition and species richness of the restored sites reflect the vegetation of the nature reserve? (3) Which ecological filters and which species traits affect the establishment of different species groups under the contrasting site conditions imposed by the treatments? (4) What can we learn from an experiment with subsequently modified treatments for grassland restoration?

2. Study area and methods

2.1 Study area and design

The study was carried out in the vicinity of the nature reserve "Garchinger Heide" in Bavaria, Germany (27 ha; 48'29° N, 11'65° E; 469 m a.s.l.; Fig. 9a), which is located in the Munich gravel plain. Mean temperature annual and precipitation are 8.7 °C and 834 mm, respectively (1980–2010; www.dwd.de, accessed 2019-03-06). Shallow, nutrient-poor Leptosols have developed on late Pleistocene calcareous gravel (Fetzer et al. 1986). The dominant plant communities of the nature reserve are the *Adonido-Brachypodietum rupestre* and the *Pulsatillo-Caricetum humilis* (Oberdorfer & Korneck 1976). In our study, the nature reserve serves as reference area and as donor site for seeds and seed-containing plant material (see below).

The experiments were conducted on three restoration fields (RF) which had been used as arable land from the beginning of the 20th century until 1993. Due to regular ploughing the topsoil had higher percentages of gravel and a lower content of organic matter; due to intensive fertilization with mineral fertilizer and sewage sludge also the concentration of exchangeable P and K in the soils of ex-arable fields were much higher compared to the nature reserve (Kiehl 2009). Two of the restoration fields

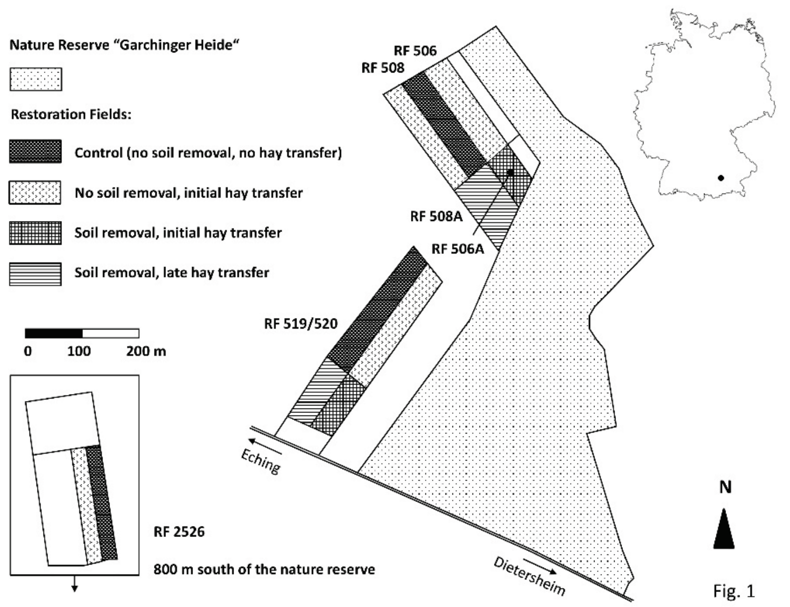

Fig. 1. Location of the restoration fields RF 506/508, RF 519/520 and RF 2526 and the reference nature reserve "Garchinger Heide". The small map shows the position of the study area in Germany.

Abb. 1. Lage der Untersuchungsflächen RF 506/508, RF 519/520, RF 2526 und des Naturschutzgebietes „Garchinger Heide", das als Referenzfläche diente. Die kleine Abbildung zeigt die Lage des Untersuchungsgebietes in Deutschland.

(RF 506/508 and RF 519/520) were adjacent to the Garchinger Heide, RF 2526 was located 800 m further south (Fig. 1, Table 1). In the year preceding the restoration in 1993, these fields had been cultivated with unfertilized cereals and their plant yield was removed to deplete nutrient levels in soil. Initially, the experiment included the treatments 'topsoil removal' (yes/no) down to the calcareous gravel and 'hay transfer' (yes/no) from the nature reserve. In 1993, 40 cm of the nutrient-rich topsoil were removed on parts of RF 506/508, and RF 519/520 respectively, but and not on RF 2526 (Table 1, Fig. 1). Between July and September 1993, seed-containing fresh hay of the nature reserve was cut approx. 4 cm above soil surface and spread out in one half of each RF, both on areas with and without topsoil removal (for details see KIEHL et al. 2006). Between 2002 and 2013, 11 Red List species that had not been established using hay transfer were collected in the nature reserve and propagated by a local seed producer. These species had not been transferred by green hay due to their small size (e.g. *Globularia* spp., *Teucrium montanum*) or early flowering and seed shed before hay collection (e.g. *Biscutella laevigata*, *Pulsatilla* spp.). A complete list of the species additionally sown including their seed densities is given in Table 2. Depending on the species, sowing was performed in late August and September of different years between 2003 and 2013. Due to the limited availability, sowing of these seeds was mainly restricted to the two sites with topsoil removal (Supplement S1), where successful establishment was expected due to a low vegetation cover < 50%. Five rare species for which propagation yielded a greater amount of seed were also sown to plots without topsoil removal and hay transfer. The sown species and their sowing densities are listed in Table 2, Table 1 provides an overview over the treatment combinations that were evaluated in this study. In fields without topsoil removal, plants rapidly achieved high cover. Therefore, regular mowing after seed shed and hay removal started already in the 2nd year after restoration. Due to their low productivity, areas with topsoil removal have not been mown yet and only shrubs were removed when necessary (KIEHL 2009).

Table 1. Overview over the restoration measures and the number of sampling plots in the three restoration fields (RF 506/508, RF 519/520 and RF 2526) which were used for vegetation (2 m × 2 m) and aboveground biomass (0.4 m × 0.4 m) sampling from 1993 to 2014. To provide sufficient power to compare the treatments in the final year statistically, additional 'random plots' were established in 2014 (indicated with a plus [+] sign).

Tabelle 1. Überblick über die Renaturierungsmaßnahmen und die Zahl der Probeflächen in den drei Erhebungsflächen (RF 506/508, RF 519/520 und RF 2526), wo von 1993 bis 2014 die Vegetation (2 m × 2 m) und die Phytomasse (0,4 m × 0,4 m) erfasst wurde. Um beim Vergleich der Varianten im Abschlussjahr eine ausreichende statistische Aussagekraft zu erzielen, wurden 2014 zufällig weitere, durch ein Plus [+] gekennzeichnete Plots eingerichtet.

Treatments	Restoration fields	Topsoil removal	Hay transfer	Sowing of Red List species	Number of plots (permanent + random plots)	Number of above-ground biomass samples (permanent + random plots)
Control	RF 508	–	–	–	20 + 2	16 + 2
	RF 519	–	–	–	10	8
	RF 2526	–	–	–	10 + 2	8 + 2
R^+M^e	RF 506 A	1993	1993	2003–2013	10 + 1	8
	RF 519/520	1993	1993	2003–2013	10	6
R^+M^l	RF 508 A	1993	2003	2003–2013	10 + 2	8 + 1
	RF 519/520	1993	2003	2003–2013	10	6
R^-M^e	RF 506/508	–	1993	–	20	16
	RF 519/520	–	1993	–	10	8
	RF 2526	–	1993	–	10	8
Nature reserve (target)		–	–	–	0 + 8	0 + 8
Total					120 + 15	92 + 13

Table 2. Species and sowing densities of Red List species additionally sown in 2003 and between 2010–2013 to fields with topsoil removal and to the control plots. *Red List status of *Teucrium montanum* is 'near threatened'.

Tabelle 2. Arten und Aussaatdichten der zwischen 2003 und 2010–2013 nachgesäten Rote Liste-Arten in Flächen mit Bodenabtrag und in den Kontrollflächen. *Rote-Liste-Status von *Teucrium montanum* ist 'Vorwarnliste'.

Species	Sowing densities (g/m²)	Plots with topsoil removal	Control plots
Aster amarellus	0.10–0.15	x	
Aster linosyris	0.10–0.15	x	
Biscutella laevigata	0.05	x	x
Centaurea triumfettii	0.11–0.20	x	
Globularia punctata	0.10	x	
Pulsatilla patens	0.14–0.30	x	x
Pulsatilla vulgaris	0.10	x	x
Scabiosa canescens	0.13	x	x
Seseli annuum	0.05–0.10	x	x
*Teucrium montanum**	0.10	x	
Veronica spicata	0.04–0.06	x	

2.2 Field sampling

To monitor treatment effects on vegetation development, 120 permanent plots with a size of 2 m × 2 m each were established in 1993 (Table 1). On plots without soil removal vegetation development was annually surveyed from 1993–2002; in plots with topsoil removal the survey started one year later as there was no vegetation present in 1993 (PFADENHAUER & KIEHL 2003). Sampling was repeated in 2006 (HUMMITZSCH 2007), and 2014 (this study). Records were performed between mid-June and mid-August and included the estimation of percentage cover of all vascular plant species as well as total cover of higher plants, mosses, litter, and bare soil. WISSKIRCHEN & HAEUPLER (1998) was used as taxonomic reference. Aboveground biomass samples (n = 105; Table 1) were cut in 40 cm × 40 cm plots 4 cm above the soil surface, dried for 48 hours at 60 °C and weighed. This was done at the peak of vegetation development at the end of July.

2.3 Data analysis

To distinguish between target and non-target species, all vascular plant species were assigned to phytosociological classes according to OBERDORFER (2001). 'Target species' included species characteristic for ancient calcareous grasslands in the study area, i. e. the classes *Festuco-Brometea*, *Trifolio-Geranietea*, *Sedo-Scleranthetea*, and *Nardo-Callunetea* (Supplement S1). 'Non-target species' were 'species of productive grassland' belonging to the *Molinio-Arrhenatheretea* class and 'ruderals' including species from the *Artemisietea*, *Chenopodietea*, *Secalietea* classes and other pioneer plants. In addition, species were grouped according to their status in the Bavarian Red List of vascular plants (SCHEUERER & AHLMER 2003; Supplement S1).

For each plot vegetation and aboveground biomass data were recorded separately. However, as permanent plots were arranged in groups of five chessboard-like adjacent to each other, they did not represent independent samples. To reduce this spatial autocorrelation, we calculated mean values for each group of five plots and used only these values as replicates for statistical analyses. As we only tested for statistical differences between treatments in the final year of the study and not along the time series, seven additional plots were randomly selected in the restoration fields in 2014 to increase the statistical power of the comparison between treatments (Table 1). Each of these random plots was used as an individual replicate. To provide a reference base for assessing the restoration success by comparing the vegetation of the experimental plots with the nature reserve in the final year another eight sampling plots were randomly established in the 'Garchinger Heide' area.

To evaluate differences between the treatments and the reference site in 2014 we conducted permutation-based two-sample t-tests with 9999 randomizations (perm.t.test in R) which do not assume normality or homogeneity of variance (MOORE et al. 2016). Bonferroni corrections were calculated to prevent inflation of alpha error (ABDI 2007). Changes in the species composition from 1993 to 2014 were visualized using a Detrended Correspondence Analysis (DCA; HILL & GAUCH 1980). The calculation was performed with square root transformed cover values of the species.

To characterize the functional composition of the vegetation we analyzed the specific leaf area (SLA), canopy height, seed mass, and seed longevity using data from the LEDA database (KLEYER et al. 2008). These traits are related to establishment and persistence, which are major challenges for re-establishment and survival after habitat restoration (PIQUERAY et al. 2015). The analyses on the functional traits were performed with original trait values except for seed mass, where values were log-transformed to achieve normal distribution. For each trait measured on a continuous scale, community weighted mean values (LAVOREL et al. 2008) were calculated by summing up all species' products of their trait value and their relative cover, and for categorical variables by summing up all species' relative cover of each category. THOMPSON et al. (1997) provide information on the persistence of seeds for species of Northwestern Europe with longevity classes from 'transient' to 'persistent'. The seed longevity index was calculated according to THOMPSON et al. (1998) by dividing the proportion of persistence proofs by the total number of records.

Data analysis was performed in R (R-CORE-TEAM 2014) using the packages 'vegan' (OKSANEN et al. 2015), 'Deducer' (FELLOWS 2012), 'RVAideMemoire' (HERVÉ 2015) and 'FD' (LALIBERTÉ et al. 2014).

3. Results

3.1 Vegetation cover and productivity

Twentyone years after the start of the restoration, aboveground biomass and plant cover of topsoil-removal plots were significantly lower than the values observed in the other treatments and neither immediate nor late hay transfer or additional sowing affected this difference (Fig. 2a und 3). In contrast, moss cover was significantly higher in plots with soil-removal (Fig. 2b). While higher levels of litter cover occurred at sites without topsoil removal and initial hay transfer, bare ground was more often observed on plots with topsoil removal and late hay transfer (Fig. 2c–d). Generally, after 21 years, vegetation cover and productivity of plots without topsoil removal were quite similar to the nature reserve 'Garchinger Heide', but differed from topsoil-removal plots.

The temporal development differed between treatments, too. Without topsoil removal, vascular plants achieved high cover in only two years. In contrast, topsoil removal led to a very slow vegetation development with cover values below 50% even after 21 years (Fig. 2 e–h). While litter cover achieved an interim maximum on plots with topsoil removal, moss cover showed a temporary increase on plots with hay transfer in 2006 but decreased until 2014. At the end of the study, cover of mosses and litter both gradually converged towards the level of the nature reserve. The percentage of bare soil decreased in all treatments.

3.2 Species richness and target species

In 2014, 89 calcareous grassland species, 23 species of productive grasslands, and 29 species of other habitat types occurred in the sampling plots (Supplement S1). Nine species were exclusively found in the nature reserve. Even 21 years after the start of restoration the number and cover of target species per plot still did not reach the level of the ancient grassland in most of the plots, but variance was high among treatments (Fig 4a). The only exception was the treatment topsoil removal with initial hay transfer and additional sowing of Red List species, where the mean number of target species per plot was similar to the nature reserve. The lowest numbers of target species were found in the control plots without topsoil removal and hay transfer. Both initial and late hay transfer clearly favored the establishment of target species (Fig. 4e). While 9 out of the 11 additionally sown Red List species established successfully (Supplement S1), only two, *Aster amellus* and *A. linosyris*, were not detected in the restoration plots. In the control plots, only one out of five sown species, *Scabiosa canescens*, was recorded. Nevertheless, also the control plots showed a slow but continuous increase of both the number of target species and the overall species richness. While ruderal species considerably increased during the first years after restoration, they almost disappeared with ongoing succession. On plots without topsoil removal, the number of species of productive grassland continuously exceeded values observed in the ancient grassland and in topsoil removal plots. Total species richness per 4 m² ranged from 21.9 in plots with topsoil removal and delayed hay transfer to 32.8 without soil removal and initial hay transfer. Significant differences, however, were rare due to variation within the different treatments.

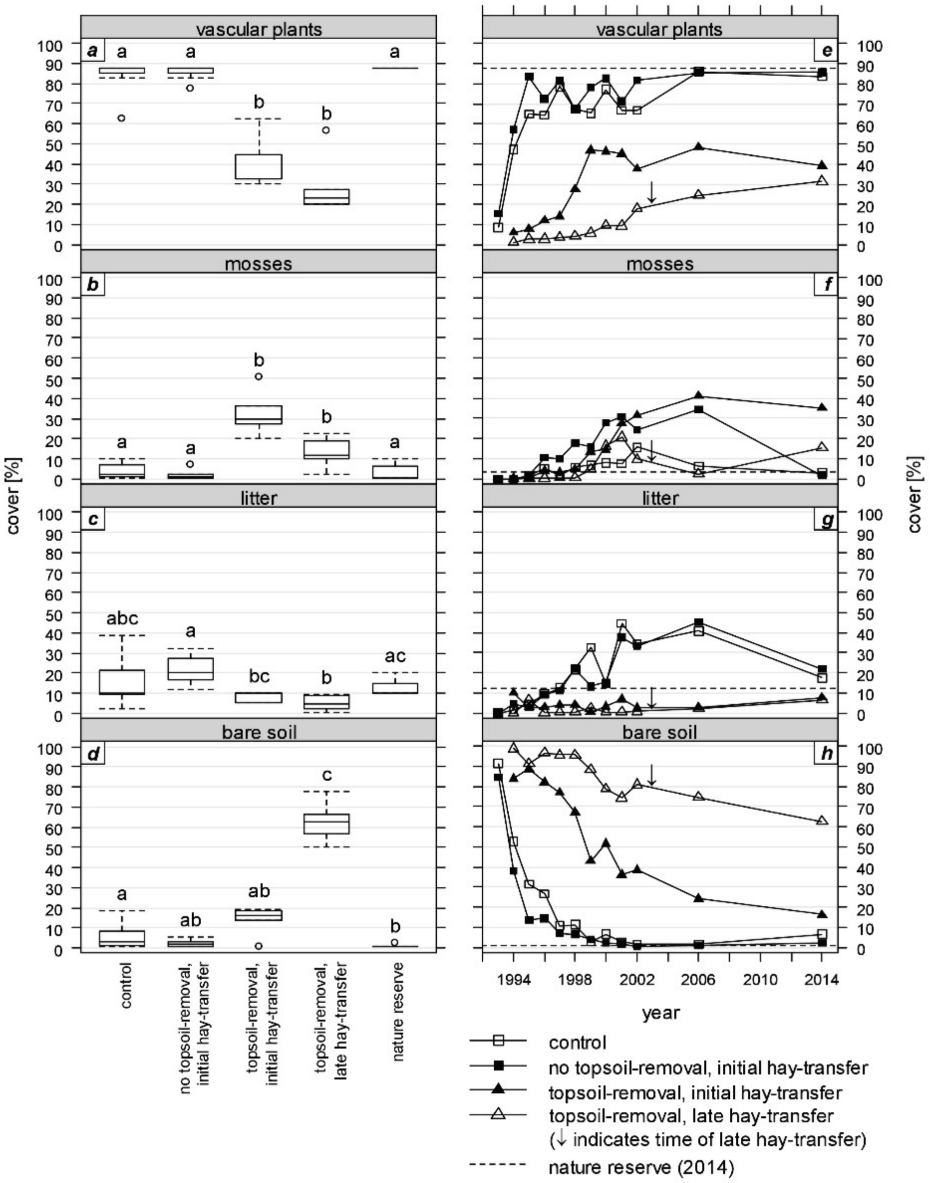

Fig. 2. Differences in 2014 **(a–d)** and temporal development 1993–2014 **(e–h)** of the mean cover of vascular plants, mosses, litter and bare ground in permament plots of the different restoration treatments and the nature reserve "Garchinger Heide". Different letters above the boxplots indicate significant differences ($p < 0.05$) in permutational t-tests with Bonferroni correction.

Abb. 2. Unterschiede im Jahr 2014 **(a–d)** und zeitliche Entwicklung 1993–2014 **(e–h)** der mittleren Deckung von Gefäßpflanzen, Moosen, Streu und offenem Boden auf den Dauerflächen der verschiedenen Renaturierungsvarianten und im Naturschutzgebiet „Garchinger Heide". Verschiedene Buchstaben stehen für signifikante Unterschiede ($p < 0{,}05$; permutationsbasierter T-Test mit Bonferroni-Korrektur).

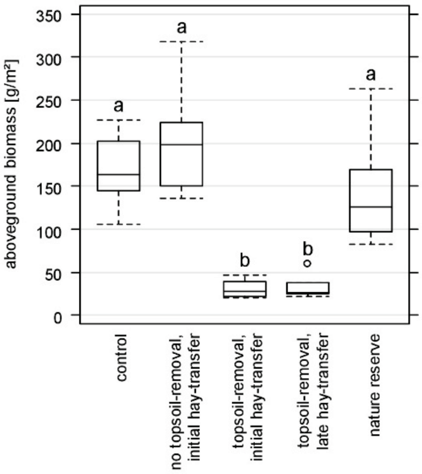

Fig. 3. Aboveground biomass (dry weight) in the different restoration treatments and in the nature reserve in 2014. Different letters indicate significant differences in permutational t-tests with Bonferroni correction ($p < 0.05$).

Abb. 3. Trockengewicht der oberirdischen Phytomasse im Naturschutzgebiet und in den unterschiedlichen Renaturierungsvarianten im Jahr 2014. Verschiedene Buchstaben stehen für signifikante Unterschiede ($p < 0,05$; permutationsbasierter T-Test mit Bonferroni-Korrektur).

Nineteen Red List species were recorded in the experimental plots, i. e. *Allium carinatum* ssp. *carinatum*, *Biscutella laevigata* ssp. *kerneri*, *Carex ericetorum*, *Centaurea triumfettii* (Fig. 9c), *Chamaecytisus ratisbonensis*, *Coronilla vaginalis*, *Dorycnium germanicum*, *Filipendula vulgaris*, *Globularia punctata*, *Inula hirta*, *Linum perenne*, *Potentilla incana*, *Pseudolysimachion spicatum*, *Pulsatilla patens*, *P. vulgaris* ssp. *oenipontana*, *Scabiosa canescens*, *Seseli annuum*, *Thesium linophyllon*, and *Veronica austriaca* ssp. *austriaca* (Supplement S1). Four threatened species (*Adonis vernalis*, *Asperula tinctoria*, *Aster linosyris* and *Rhamnus saxatilis*) were additionally detected outside the experimental plots. Thus, a total of 23 out of 61 Red List species of the reserve established successfully on the restoration fields. Whereas numbers of Red List species in plots with topsoil removal and sowing of rare species did not significantly differ from the plots in the nature reserve, values recorded in fields without topsoil removal were significantly below this reference level (Fig. 5). When the Red List species additionally sown to the restoration fields are factored out, numbers of Red List species of all restoration treatments fell significantly below the values recorded at the reference site (not figured).

3.3 Species composition

The gradient length of the first DCA-axis was 5.81 and indicated a complete species turnover (Leyer & Wesche 2007) from weed-dominated plant assemblages in 1993/94 to communities of calcareous grassland in 2014 (Fig. 6 und 7, Supplement S1). Both topsoil removal and hay transfer substantially accelerated this development. At the end of the study, the species composition of plots with topsoil removal and initial hay transfer was most similar to that of the nature reserve. Until 2002, the species composition of plots with topsoil

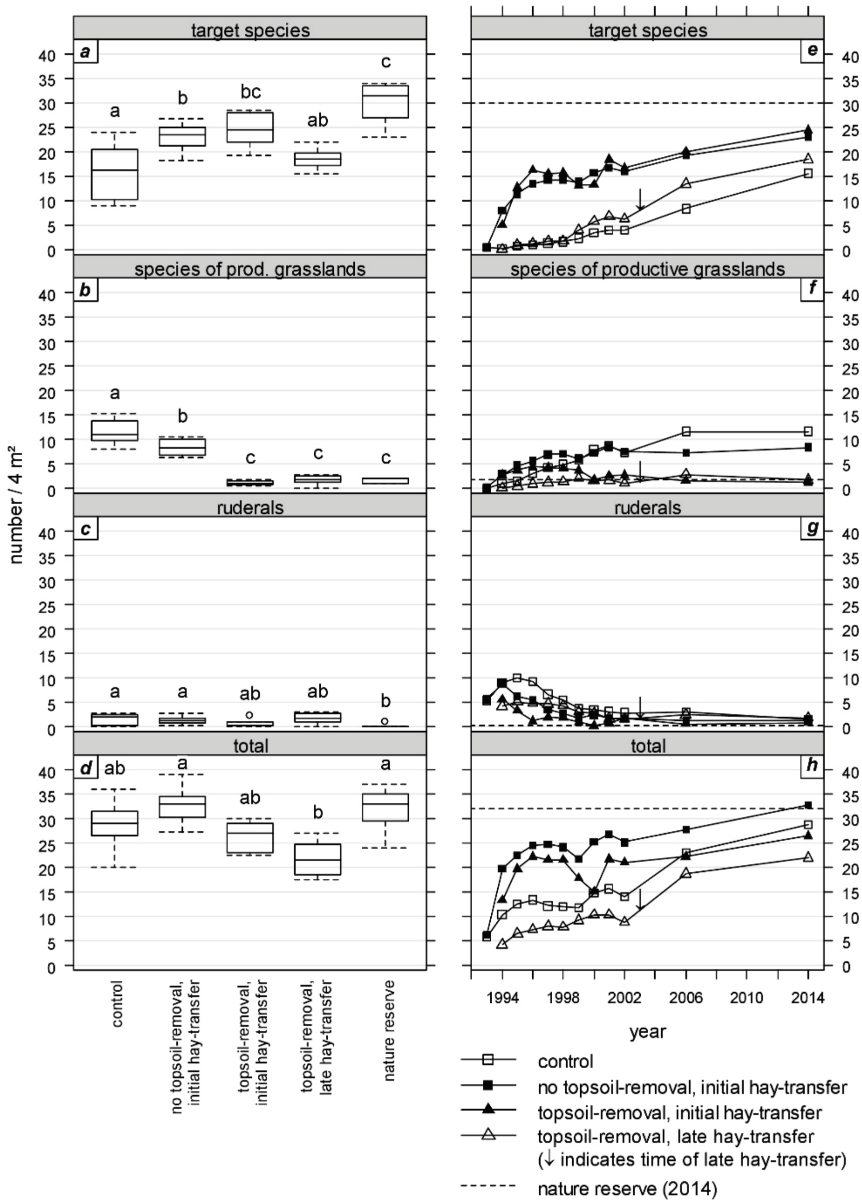

Fig. 4. Differences in 2014 **(a–d)** and temporal development 1993–2014 **(e–h)** of the mean number of target species, of ruderals and productive grassland species. Different letters above boxplots indicate significant differences between the mean number of species per 4 m² in different restoration treatments and in the nature reserve based on permutational t-tests with Bonferroni correction ($p < 0.05$).

Abb. 4. Unterschiede im Jahr 2014 **(a–d)** und zeitliche Entwicklung 1993–2014 **(e–h)** der mittleren Artenzahl pro 4 m² und der mittleren Anzahl kalkmagerrasentypischer Zielarten, Arten des Wirtschaftsgrünlandes und der Ruderalfluren. Verschiedene Buchstaben stehen für signifikante Unterschiede ($p < 0,05$; permutationsbasierter T-Test mit Bonferroni-Korrektur).

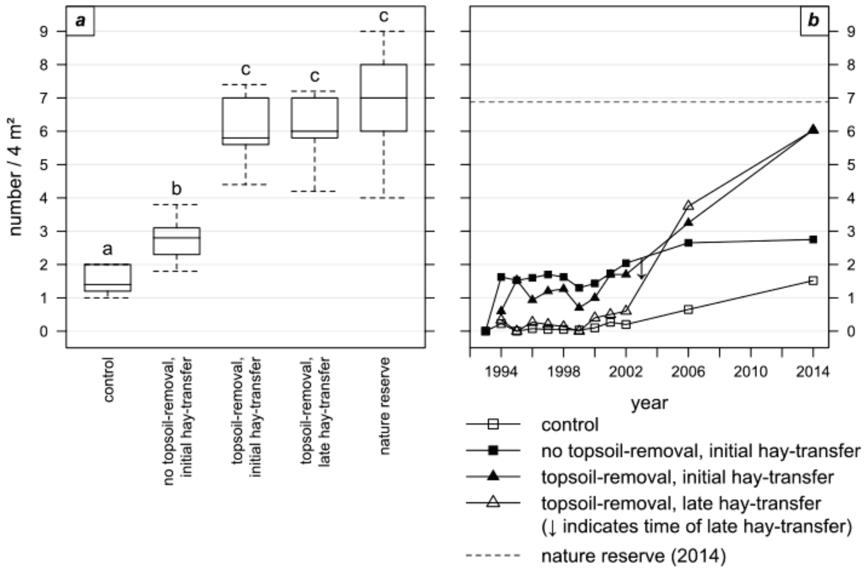

Fig. 5. Differences in 2014 and temporal development 1993–2014 of the number of Red List species per 4 m² in plots of the restoration treatments and the nature reserve "Garchinger Heide"(Red List of Bavaria; SCHEUERER & AHLMER 2003). Different lower case letters indicate significant differences in permutational t-tests with Bonferroni correction ($p < 0.05$).

Abb. 5. Unterschiede im Jahr 2014 und zeitliche Entwicklung 1993–2014 der Anzahl gefährdeter Pflanzenarten (pro 4m²) in den einzelnen Renaturierungssvarianten und im Naturschutzgebiet „Garchinger Heide" und (Rote Liste von Bayern; SCHEUERER & AHLMER 2003). Verschiedene Buchstaben stehen für signifikante Unterschiede ($p < 0{,}05$; permutationsbasierter T-Test mit Bonferroni-Korrektur).

removal and late hay transfer differed strongly from that of all other plots. After the hay transfer in 2003, the vegetation development turned in the direction of the plots with topsoil removal and initial hay transfer and proceeded towards the reference plots in the nature reserve. In comparison to the topsoil-removal plots, the vegetation of plots with hay transfer but without topsoil removal showed lower similarity to the plant community of the nature reserve. The vegetation of the untreated control plots showed a similar but considerably slower development in the direction of the treatment with hay transfer and without topsoil removal.

3.4 Functional composition

During the first 10 years of the study, the proportion of species with a high specific leaf area (SLA) declined in all treatments (Fig. 8). Over the following years, however, SLA in treatments without topsoil removal remained at the level of the nature reserve while it fell significantly below this threshold in topsoil removal plots. In plots with topsoil removal and hay transfer canopy height was similar to the nature reserve, but the other treatments promoted taller plants. The mean seed mass of species recorded in most of the restoration treatments was significantly lower than the values observed for species of the nature reserve;

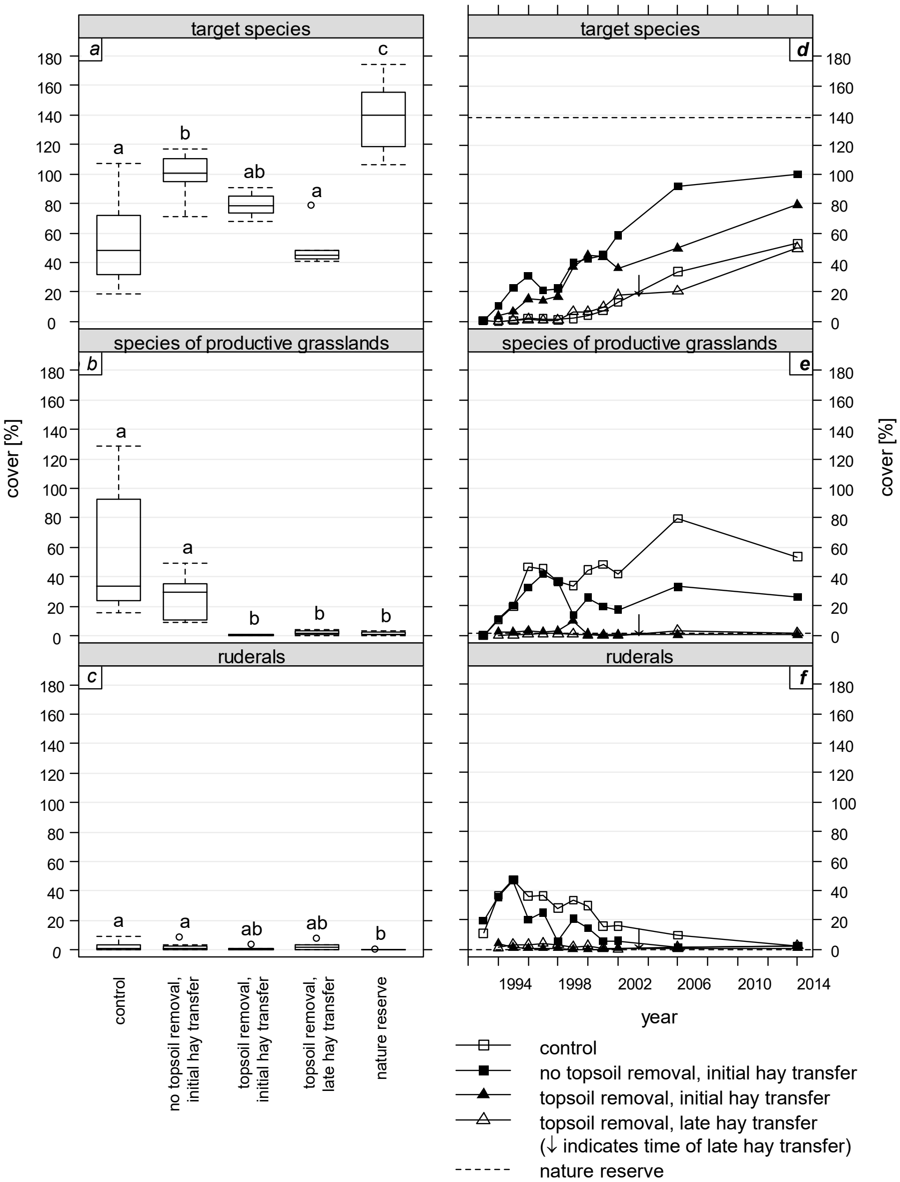

Fig. 6. Differences in 2014 **(a–c)** and temporal development 1993–2014 **(d–e)** of the total cover of target species, of species typical for productive grasslands, and of ruderal species in the nature reserve and in the different restoration treatments. Differing lower case letters indicate significant differences in pairwise permutation-based t-tests and Bonferroni corrections of alpha errors ($p < 0.05$).

Abb. 6. Unterschiede im Jahr 2014 **(a–c)** und zeitliche Entwicklung 1993–2014 **(d–f)** der Gesamtdeckung der Zielarten, typischer Arten des Wirtschaftsgrünlandes und der Ruderalfluren in den verschiedenen Renaturierungsvarianten. Unterschiedliche Buchstaben indizieren signifikante Unterschiede ($p < 0{,}05$) bei permutationsbasiertem Zweistichproben t-Test mit Bonferroni-Korrektur des Alphafehlers.

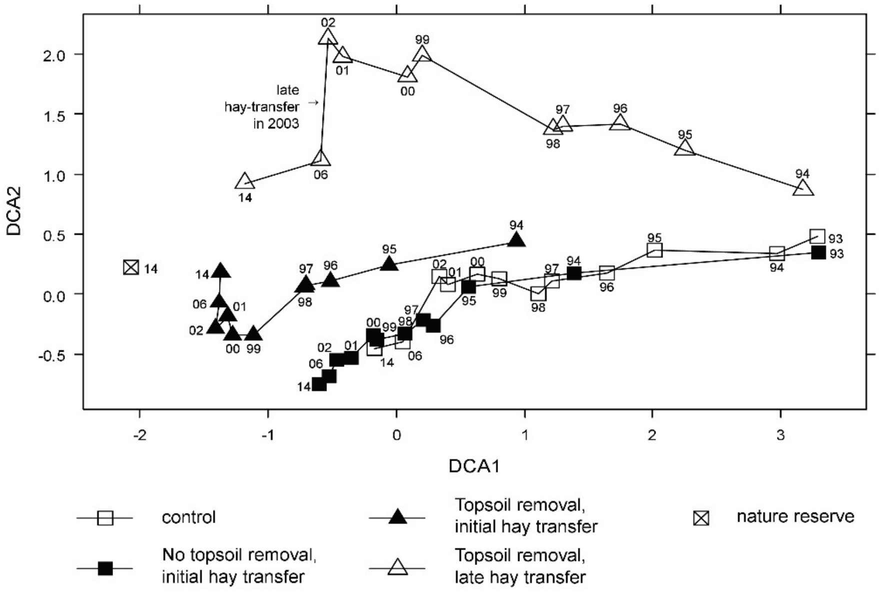

Fig. 7. Detrended Correspondence Analysis (DCA) showing the temporal development of the plant species composition in the four different restoration treatments since their establishment in 1993 in comparison to the nature reserve (reference area). Lines connect the same treatment over the years, numbers indicate the years of sampling (1993–2014). As scale marks along the Axes reflect average standard deviation of species turnover (HILL & GAUCH 1980), the length of Axis 1 of 5.81 SD units indicates an almost complete species turnover. Axis 1 and 2 explain 56.3% and 26.6% of the total variation.

Abb. 7. Detrended Correspondence Analysis (DCA) zur zeitlichen Entwicklung der Artenzusammensetzung in den vier Renaturierungsvarianten von 1993 bis 2014 im Vergleich zum Naturschutzgebiet. Für die einzelnen Renaturierungsvarianten sind die Aufnahmezeitpunkte jeweils durch Linien verbunden, die Zahlen bezeichnen Jahre (1993–2014). Da die Skalierung von DCA-Achsen Standardabweichungseinheiten beschreibt (HILL & GAUCH 1980), bedeutet die Gradientenlänge 5,81 von DCA-Achse 1 einen fast vollständigen Turnover im Artenspektrum. DCA-Achse 1 erklärt 56,3 % und DCA-Achse 2 weitere 26,6 % der Gesamtvarianz.

only in plots without topsoil removal and initial hay transfer this difference was not significant. While the seed longevity index of areas with topsoil removal decreased to the level of the nature reserve, values remained significantly above this reference where the arable soil had not been removed.

4. Discussion

4.1 Vegetation cover and productivity

Vegetation cover and aboveground biomass are attributes that reflect nutrient status and interspecific competition within ecosystems. In our study, vascular plant cover, aboveground biomass, and litter cover of ex-arable fields without topsoil removal rapidly reached the level of the target vegetation in the nature reserve. Presumably, this was because the nutrient rich

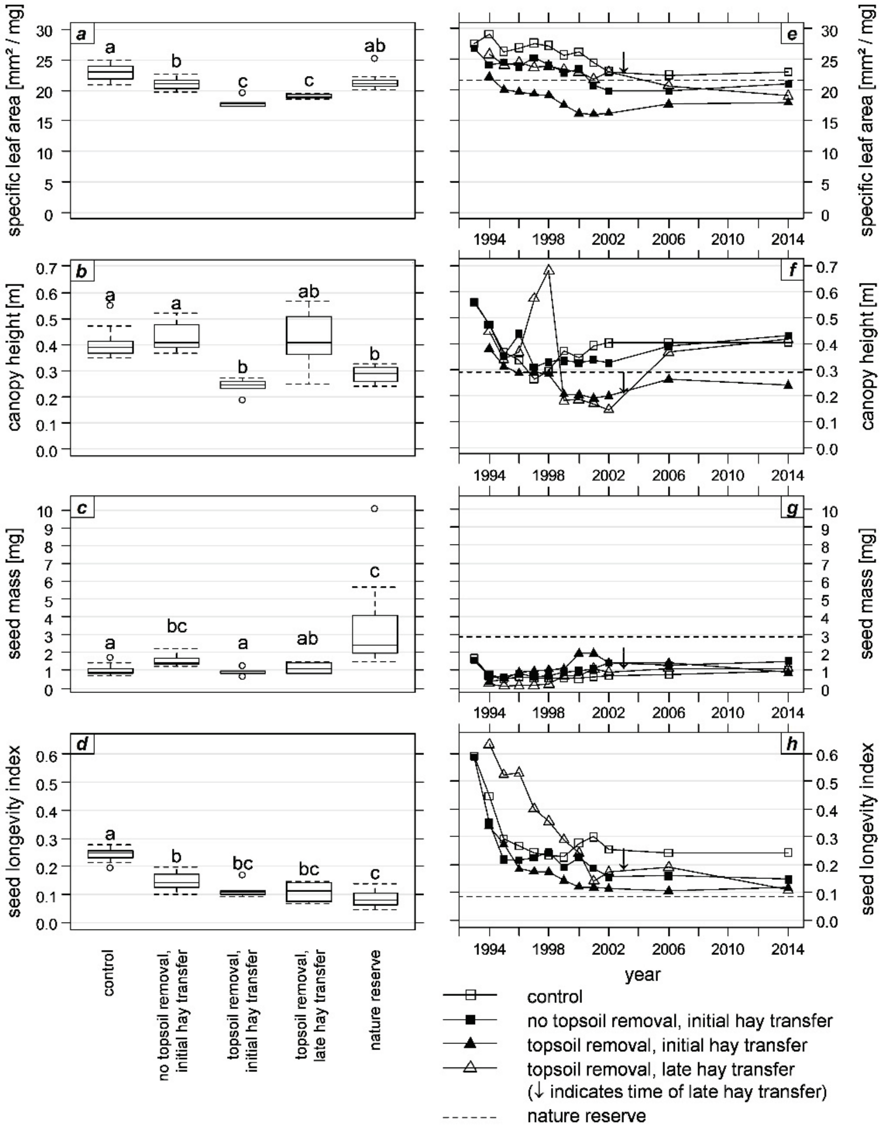

Fig. 8. Differences in 2014 **(a–d)** and temporal development **(e–h)** of specific leaf area, canopy height, seed mass, and seed longevity in plots of the different restoration treatments and the nature reserve. Differing lower case letters indicate significant differences in pairwise permutational t-tests and Bonferroni corrections of alpha errors ($p < 0.05$).

Abb. 8. Unterschiede im Jahr 2014 **(a–d)** und zeitliche Entwicklung **(e–h)** der spezifischen Blattfläche, Wuchshöhe, Samenmasse und Lebensdauer der Samen in den Dauerflächen der verschiedenen Renaturierungsvarianten und im Naturschutzgebiet. Verschiedene Buchstaben indizieren signifikante Unterschiede ($p < 0,05$) bei permutationsbasiertem Zweistichproben T-Test mit Bonferroni-Korrektur des Alphafehlers.

topsoil provided both suitable conditions for the survival of the soil seed bank and for the establishment of anemochorous and hay transferred propagules. Nonetheless, even 21 years after the establishment, dry matter production of restoration fields without topsoil removal did not exceed the upper limit of 350 g/m² for low productive grassland (SCHIEFER 1984). On plots with topsoil removal aboveground biomass still remained below 100 g/m² and median vegetation cover did not exceed 50%. The great depth of topsoil removal and the low fertility of remaining substrates were probably the reason for this limited vegetation development (KIEHL et al. 2003, KIEHL & PFADENHAUER 2007). In our study, fine grained topsoil was completely removed and hay and seeds were spread on bare gravel. Consistently low vegetation cover even on plots with initial hay transfer suggests that the vegetation there will not achieve complete cover and thus site conditions will promote the persistence of stress-tolerant low-growing plants on the long term. The high moss cover on our topsoil removal sites indicates that mosses cope well with these extreme conditions (JESCHKE & KIEHL 2006). On the long term, however, this high moss cover could also affect further regeneration of vascular plants (JESCHKE & KIEHL 2008, DONATH & ECKSTEIN 2010, HUBER & KOLLMANN 2019).

4.2 Development of the species diversity

In our study, the successful establishment of 89 species of calcareous grassland 21 years after start of the restoration verifies a careful and efficient species transfer (EDWARDS et al. 2007, PYWELL et al. 2003). This number refers only to species found on the 4 m² plots and is therefore lower than the number of 102 vascular plant species of the nature reserve which were detected by mapping the whole area of the restoration fields in 2006 (KIEHL 2009). Although these values indicate that the restoration was quite successful, the objective to establish the majority of the more than 200 plant species of the nature reserve site by combining measures like topsoil removal, hay transfer and sowing has not been achieved in this 21-years experiment. Reasons are that seeds of many low-growing species escaped the harvesting machines, early flowering species had already shed their seeds and seeds of late flowering species like *Anthericum ramosum* were not ripe at the time of harvest (KIEHL et al. 2006). In addition, sites of very rare species were not harvested in order to conserve their threatened populations. Only 11 of the species not transferred by hay seeds were propagated and sown additionally. Nine of these species established successfully including the very rare Natura 2000 species *Pulsatilla patens*, which could be found with more than 35,000 individuals on the restoration sites with topsoil removal in 2007 (RÖDER & KIEHL 2008).

Only in one restoration treatment, i.e. topsoil removal with initial hay transfer plus additional sowing of rare plants, the mean number of target species per 4 m² plot did not significantly differ from the plots of the reference site. On sites without topsoil removal, successful establishment was presumably limited by competition from plants of productive grassland. Due to the higher nutrient and water availability these species were favoured on restoration fields without topsoil removal and continuously made up 20–30% of the vegetation cover. As grasses like *Arrhenatherum elatius* or *Dactylis glomerata* are taller than most species of calcareous grassland, also the canopy of these plots was significantly higher compared to sites without soil removal. As tall plants usually produce large seeds and vigorous seedlings, they have much better chances to establish and to survive in a dense vegetation layer than the smaller, less competitive species of calcareous grassland (GROSS 1984, LEISHMAN 1999, VERHAGEN et al. 2001, FAGAN et al. 2008). This might have been the reason why only one out of the five rare species which had been sown into the control plots was re-detected

Fig. 9. a) Despite long-term conservation management since 1908, various target species of the Garchinger Heide reserve declined (BAUER et al. 2020). Therefore, restoration treatments were established on ex-arable fields in the surrounding area in 1993. **b)** View over the plots with topsoil removal to the nature reserve Garchinger Heide. **c)** In 2017 29 plants of *Centaurea triumfettii* were recorded in the Garchinger Heide reserve, the population estimated for the restoration fields was 1500 to 2300 (PÖLLINGER & KIEFER 2017) (Photos: H. Albrecht, May and June 2020).

Abb. 9. a) Das Naturschutzgebiet Garchinger Heide wird seit 1908 nach Artenschutzgesichtspunkten bewirtschaftet. Trotzdem zeigt eine Reihe wichtiger Zielarten eine rückläufige Entwicklung (BAUER et al. 2020), weshalb 1993 Erweiterungsflächen angelegt wurden. **b)** Blick über die Bodenabtragsparzellen zum Naturschutzgebiet Garchinger Heide. **c)** 2017 wurden auf der Garchinger Heide noch 29 Exemplare von *Centaurea triumfettii* gezählt, auf den Erweiterungsflächen wurde die Population auf zwischen 1500 und 2300 Individuen geschätzt (PÖLLINGER & KIEFER 2017). Die Garchinger Heide ist das einzige bekannte vorkommen in Deutschland (Fotos: H. Albrecht, Mai und Juni 2020).

there. This result suggests that dense vegetation and litter cover and a lack of suitable gaps for germination may significantly reduce the chance of such species to establish successfully. Such poor establishment in fields without topsoil removal is confirmed by SMITH et al. (2017) who sowed different seed mixtures to establish calcareous grassland in an abandoned limestone quarry where stony raw material was covered with local topsoil. Seventeen years later the species composition of our plots without soil removal rather resembled mesotrophic grassland communities and did not achieve strong resemblance to the target. Although the target to restore calcareous grassland on our fields without topsoil removal has been missed, also the establishment of dry mesophytic grassland can be seen as a success. From a nature conservation perspective, such dry and species rich forms of the *Arrhenatherion* community represent highly valuable plant assemblages which are highly endangered in Germany and protected as Natura 2000 habitat type within the European Union (TISCHEW et al. 2018).

Our ordination results confirm von Blanckenhagen & Poschlod (2005) and Piquer-ay et al. (2011), who observed increasing floristic similarity between reference sites and restored calcareous grasslands with advancing duration of restoration. In our study, however, similarity to the reference site varied between treatments. The species composition closest to that of the nature reserve occurred on topsoil removal plots. Many typical calcareous grassland species which tolerate drought particularly profited from these establishment conditions and largely contributed to this similarity. Recently, however, this convergence considerably decelerated. This could be caused by less favourable conditions for the more mesophytic species of calcareous grassland which usually contribute to target vegetation but lack in the plots with topsoil removal.

If strong resemblance between donor and target site is the objective of restoration, the transfer of seeds is of crucial importance (Verhagen et al. 2001). Thus, the germination capacity of the seeds introduced by hay has decisive influence on restoration success. Therefore, an important prerequisite to efficiently transfer of seeds is that hay with mature seeds is harvested shortly before seed shedding. As time of seed ripening varies from species to species, this may require several harvest campaigns (Kiehl et al. 2006).

In our study, the additional sowing of selected threatened species has proved to successfully overcome dispersal limitation which frequently constrains restoration of dry grassland (Hutchings & Booth 1996, Pywell et al. 2003, Edwards et al. 2007). However, although sowing clearly contributed to a greater similarity between plots with topsoil removal and the donor site, this measure could also hamper further convergence. Hence, species like *Globularia punctata* or *Centaurea triumfettii*, which are restricted to a few small patches in the nature reserve, are well established now on sites with topsoil removal, where competition is lower than in the denser vegetation of the ancient grassland. In contrast, other sown species like *Aster amellus* and *A. linosyris* did not establish so far. As these species have a cs or csr life strategy (Klotz et al. 2002), they may be less susceptible to competition and might have profited more from seeding on the fertile substrates of treatments without topsoil removal. This varying degree of establishment confirms the essential importance of creating species specific microsites which are suitable for the germination and growth of seedlings (Kahmen et al. 2002).

Nevertheless, even in plots without specific measures to enhance diversity the number of target species and the overall species richness continuously increased. As only a few individuals of one additionally sown rare species (*Scabiosa canescens*) successfully established under the close canopy of the control plots, the effect of this measure on vegetation development was almost negligible here. Analysing the results of various long term restoration projects Fagan et al. (2008) observed that, over a long time-scale, naturally regenerated sites became even more similar to the established calcareous grassland than sites with targeted species transfer. However, natural regeneration was only successful in the direct proximity of ancient and well preserved grasslands (Fagan et al. 2008, Conradi & Kollmann 2016). Although target species also started to colonize the untreated control plots in our study, establishment was much faster in plots with initial hay transfer. The trajectories in Figure 6 show that this rapid increase mainly occurred during the initial decade after restoration and slowed down afterwards. Rydgren et al. (2019) also observed that compositional recovery of the target vegetation usually decreased with time since restoration.

At the actual stage, it is difficult to predict how the species composition of the fields with different treatments will develop in the long-term. Hence, sites with topsoil removal performed quite well but they will possibly never inhabit plant communities which exactly reflect the ancient grassland. With the removal of fine grained soil particles (which determine nutrient richness and water holding capacity in mineral soils) the life conditions may have changed from typical calcareous grassland to an environment more suitable for xerophytic plants. The study of FAGAN et al. (2008) suggests that plots without topsoil removal, hay transfer and seeding once could host plant assemblages close to the target site - despite the fact that they actually harbor the lowest numbers of target species. At our study fields former application of sewage sludge (KIEHL et al. 2003) question the success of this strategy, however. In general, conservation managers should be aware that topsoil removal generates site conditions which are different to "normal" calcareous grassland by selectively favouring stress tolerant plants. In our study, different treatments on adjacent sites created diverse conditions for different target species with contrasting habitat requirements. Hence, the combination of different treatments is a suitable strategy to establish larger numbers of target species (CONRADI & KOLLMANN 2016).

4.3 Trait composition

Both, the comparison of treatments and the analysis of the temporal development showed that traits from species present on restoration fields still differed from those of the target vegetation in the nature reserve. As plants typical for habitats with frequent drought usually have low SLA, significantly lower values in plots with topsoil removal reflect a strong selection for drought tolerance (REICH et al. 1992, WESTOBY 1998). During the initial phase of the transition from arable fields to dry grassland, the SLA of these plots even fell below the values of the nature reserve and showed no further change over the last eight years. This development suggests that the further convergence between the vegetation of the reserve and the fields with topsoil removal will probably progress very slowly in the future.

Species from habitats with frequent soil disturbance like ruderals or arable weeds usually produce small seeds with a pronounced longevity (THOMPSON et al. 1998). Therefore, a significant increase in seed mass and a decrease in seed longevity could be expected after the transition from arable to grassland use (ALBRECHT & AUERWALD 2009). In our study both expectations were fulfilled. However, in most restoration plots these reproduction traits still showed significant differences to the target vegetation. This was mainly due to a higher proportion of ruderal species at sites without topsoil removal and higher percentages of stress tolerant species at sites with topsoil removal which both usually have smaller seeds and a higher seed longevity (BEKKER et al. 1998, THOMPSON et al. 1998). Our results indicated that even 21 years after the implementation of restoration measures, the functional composition of the plant assemblages still differed from the target vegetation. These differences were more pronounced in traits which reflect the life conditions of species concerning adaptation to drought, competition and reproduction. Immediately after restoration most of these traits showed a clear trajectory towards the target vegetation, but during the second decade this approximation considerably slowed down, which means that these differences might also persist on the long run. Our results also confirm ENGST et al. (2016) who observed that trajectories of different functional traits to the reference proceed at a different pace.

5. Conclusions

From a conservation perspective one might ask whether it is reasonable to aim at establishing a species composition as similar as possible to the donor site. An alternative goal may be to provide optimal habitat conditions for a subset of rare or characteristic species that are declining. For instance, some small and low-competitive Chamaephytes may hardly become established in the dense turf of the reference site, but thrive under the open conditions of restoration sites with topsoil removal. In our study achieving similarity between restoration and the donor site was attempted because - like in other reserves with high nature conservation value - the Garchinger Heide itself shows a decline in the overall species diversity and in the populations of various target species (Bauer et al. 2020). Under such conditions, expanding the potential habitat of the local plant community by actively transferring as many of the typical species as possible seems to be an adequate way to counteract further losses. However, it is hardly possible to prepare soil conditions on ex-arable land which are almost identical to those of ancient calcareous grassland. Hence, we suggest that a combination of different restoration treatments might be a promising strategy to create a broad range of habitat conditions for a large number of target species. Regarding the number of target species, plots with top-soil removal, initial hay transfer and additional sowing of rare species performed best and did not significantly differ from the nature reserve after 21 years. However, also variants without hay transfer and topsoil removal showed a steady increase of target species which might once harbor the species assemblage most similar to the nature reserve as was found for calcareous grasslands restored by Fagan et al. (2008) in the UK. Regarding the development of individual species, the Natura 2000 species *Pulsatilla patens* even achieved higher population densities on the restoration fields than at the donor site (Bauer et al. 2020).

What are the consequences for nature conservation? Critical readers may complain that different restoration treatments were mixed in a way that the experimental design was confounded and the success of individual measures became blurred. During the first decade, this project followed a two-factorial design with or without topsoil removal and hay transfer, respectively. Once it turned out that treatments like 'topsoil removal without hay transfer' showed no satisfying balance between costs and establishment of target species, it was decided to give up the factorial design and to improve restoration success by further transferring fresh seed-containing hay and by seeding rare species which had not established yet. For practitioners, this procedure rather leads to information on the effect of combining different treatments than to provide recommendations for certain treatments. The highest degree of similarity between ancient and restored calcareous grassland in literature was observed by Fagan et al. (2008), who found an increasing overlap between restored and ancient grassland communities with time since restoration. However, differences were still significant even after 60 years. The dynamic approach realized in our project, i.e. initially establishing differing treatments combined in a factorial design, then evaluating the establishment success and finally adjusting the variants with sub-optimal development by additional transfer of fresh seed containing hay and seeding some rare species may be an option to establish species rich grassland of high conservation value in a far shorter time. Another advantage of this strategy is that the spread of undesired species like competitive grasses or ruderals can be controlled more easily.

Erweiterte deutsche Zusammenfassung

Einleitung – Da von den einst großen Kalkmagerrasengebieten Mitteleuropas heute oft nur kleine und isolierte Reste übrig sind, gelten viele der auf diesen Lebensraum spezialisierten Arten als gefährdet (FISCHER & STÖCKLIN 1997, KRAUSS et al. 2010). Da bestehende Kalkmagerrasen zudem oft durch Nutzungsintensivierung oder Nutzungsaufgabe degradiert sind (WILLEMS 2001, POSCHLOD & WALLIS-DEVRIES 2002), ist der Schutz bestehender Flächen allein nicht ausreichend (EUROPEAN COMMISSION 2007). Deshalb ist es zunehmend notwendig, Magerrasen mit hohen Anteilen lebensraumtypischer Arten aktiv wiederherzustellen (FAGAN et al. 2008, TÖRÖK et al. 2011). Die meisten Pflanzenarten der Kalkmagerrasen verfügen weder über persistente Samenvorräte noch über effiziente natürliche Fernausbreitungsmechanismen (HUTCHINGS & BOOTH 1996, MAURER et al. 2003, DIACON-BOLLI et al. 2013, CONRADI & KOLLMANN 2016). Zudem sind auch traditionelle Beweidungssysteme wie die Transhumanz, die früher maßgeblich zur (Fern-)Ausbreitung beigetragen haben (WAGNER et al. 2013, RICO et al. 2014), verschwunden. Eine erfolgreiche Re-Etablierung lebensraumtypischer Zielarten aus dem Bodensamenvorrat oder von umliegenden Flächen ist somit unwahrscheinlich, was eine gezielte Wiederansiedlung von Zielarten erfordert (KIEHL et al. 2010). Die Übertragung von diasporenhaltigem Mähgut ist dabei besonders vorteilhaft: Es enthält viele Samen erwünschter Arten, erhält den regionalen Genpool, schützt die Samen vor Austrocknung und die Methode ist preisgünstig und leicht umsetzbar (KIEHL et al. 2010, TÖRÖK et al. 2011). Ein besonderes Problem bei der Renaturierung von Ackerflächen ist, dass hohe Nährstoffkonzentrationen und große Samenvorräte konkurrenzkräftiger Unkräuter den Etablierungserfolg gefährden können (VERHAGEN et al. 2001). Oberbodenabtrag gilt hier als effiziente Methode, um sowohl hohe Nährstoffbelastungen als auch die Bodensamenvorräte unerwünschter Arten zu reduzieren (VERHAGEN et al. 2001, BAKKER et al. 2012).

Die vorliegende Studie stellt Ergebnisse zur langfristigen Entwicklung der Vegetation neu angelegter Kalkmagerrasen auf Ackerflächen im Umfeld der Garchinger Heide in der nördlichen Münchner Schotterebene über einen Zeitraum von 21 Jahren vor. Dort wurden Oberbodenabtrag, Mähgutübertragung und die ergänzende Einsaat gefährdeter Arten zu verschiedenen Renaturierungsvarianten kombiniert. Das 27 ha große Naturschutzgebiet „Garchinger Heide" enthält 61 höhere Pflanzenarten, die in der Roten Liste Deutschlands (BfN 2018) oder Bayerns (SCHEUERER & AHLMER 2003) als gefährdet eingestuft sind. Da die artenreichen Kalkmagerrasen (*Adonido-Brachypodietum rupestre* und *Pulsatillo-Caricetum humilis,* OBERDORFER & KORNECK 1976) dort durch Umweltveränderungen zunehmend bedroht sind (BAUER et al. 2020), wurden 1993 auf benachbarten Äckern Kalkmagerrasen neu angelegt. In der vorliegenden Untersuchung sollten folgende Fragen beantwortet werden: (1) Wie erfolgreich konnten sich typische Arten der Kalkmagerrasen (= Zielarten) in den verschiedenen Renaturierungsvarianten etablieren? (2) Inwieweit entspricht die Zusammensetzung und Vielfalt der neu etablierten Artengemeinschaften der Vegetation der Spenderfläche? (3) Welche ökologischen Filter und welche Arteigenschaften beeinflussen die Etablierung unterschiedlicher Artengruppen in den verschiedenen Renaturierungsvarianten? (4) Welche Rückschlusse lassen sich aus einem Versuch zur Renaturierung von Kalkmagerrasen ziehen, bei dem die Behandlungen während der Laufzeit nachgebessert wurden?

Methoden – Auf ehemaligen Ackerflächen im Umfeld des NSG „Garchinger Heide" wurden vier Renaturierungsvarianten untersucht: (1) ohne Bodenabtrag und ohne Mähgut (Kontrolle), (2) ohne Bodenabtrag und mit sofortiger Mähgutübertragung 1993, (3) mit 40 cm Oberbodenabtrag (1993) und sofortiger Mähgutübertragung und (4) mit Oberbodenabtrag (1993) und Mähgutübertragung 10 Jahre später. Das Mähgut wurde jeweils im NSG „Garchinger Heide" gewonnen und in frischem Zustand auf die Empfängerflächen übertragen (KIEHL et al. 2006). Darüber hinaus wurden zwischen 2003 und 2013 insgesamt 11 nicht mit dem Mähgut übertragene Rote Liste-Arten zwischenvermehrt und ausgesät. Wegen der geringen Saatgutmengen erfolgte diese Ausbringung hauptsächlich auf den Flächen mit Oberbodenabtrag, wo eine Vegetationsdeckung < 50 % gute Etablierungschancen versprach (Arten und Saatdichten siehe Beilage S1). Fünf der seltenen Arten wurden auch auf Flächen ohne Oberbodenabtrag und ohne Mähgut ausgebracht. Als Referenzflächen für die Bewertung des Renaturierungserfolgs dienten die primären Kalkmagerrasen des Naturschutzgebiets. Funktionale Merkmale der Pflanzenarten wie spezifische Blattfläche, Pflanzenhöhe sowie Gewicht und Lebensdauer der Samen sollten die Anpassung der Pflanzenbestände an die jeweiligen Umweltbedingungen aufzeigen (WEIHER et al. 1999, WESTOBY et al. 2002).

Insgesamt wurden 120 Dauerflächen mit einer Größe von je 2 m × 2 m angelegt. Sie wurden von 1993 bis 2002 jährlich (PFADENHAUER & KIEHL 2003) und danach noch 2006 (HUMMITZSCH 2007) und 2014 (diese Studie) untersucht. Die Deckung der Einzelarten und die Gesamtdeckung von höheren Pflanzen, Moosen, Streu und offenem Boden wurden erfasst. Die oberirdische Phytomasse wurde von 107 Plots aus 40 cm × 40-cm Quadraten entnommen. Die Datenanalyse umfasst die zeitliche Veränderung über 21 Jahre und die Unterschiede zwischen den Anlagevarianten und der Altheide im Jahr 2014. Da die Probeplots 1993 jeweils in Fünfergruppen anlegt worden waren, gingen in den statistischen Vergleich der Behandlungen für 2014 neben den Mittelwerten dieser fünf Plots auch einige zufällig in den entsprechenden Varianten angelegte Plots zur Erhöhung der Stichprobenzahl ein (vgl. Tab. 1).

Ergebnisse – Insgesamt wurden 89 kalkmagerrasentypische Zielarten auf den Dauerflächen der Renaturierungsparzellen nachgewiesen. Von den 61 Rote Liste-Arten des Naturschutzgebiets konnten sich 19 erfolgreich in den Probeflächen etablieren, fünf weitere Arten kamen 2014 außerhalb der Plots vor. Während die Probeflächen ohne Bodenabtrag schon nach wenigen Jahren eine ähnliche Phytomasseproduktion und Vegetationsdeckung aufwiesen wie die Altheide, lag die Deckung der Vegetation der Abtragsflächen auch nach 21 Jahren noch unter 50 %.

Die Mähgutübertragung und die Einsaat gefährdeter Arten führten zur deutlich beschleunigten Etablierung der Zielarten gegenüber den Kontrollflächen. In allen Varianten entwickelte sich die Artenzusammensetzung von Beständen, die 1993/94 durch Ruderalarten und Ackerwildpflanzen dominiert wurden, zu Pflanzengemeinschaften, die 2014 überwiegend durch Arten der Kalkmagerrasen und – bei den Flächen ohne Oberbodenabtrag – auch durch Arten des Wirtschaftsgrünlands geprägt waren. Die Bodenabtragsflächen mit Mähgut und Einsaat seltener Arten waren im Jahr 2014 dem Naturschutzgebiet am ähnlichsten. Der Oberbodenabtrag auf Kalkschotter förderte stresstolerante Arten, die in der Altheide nur subdominant vorkommen. Dieser Unterschied blieb bis zum Ende der Untersuchungen bestehen. Alle Renaturierungsvarianten mit Mähgut wiesen eine höhere Ähnlichkeit zur Spenderfläche auf als die unbehandelte Kontrolle. Auch bei den jeweils vorherrschenden funktionalen Eigenschaften der Pflanzenarten gab es nach 21 Jahren noch große Unterschiede: So war die durchschnittliche Samenmasse der Arten auf den Renaturierungsflächen deutlich geringer, deren mittlere Langlebigkeit und die Bestandshöhe war dagegen auf den meisten der neu angelegten Parzellen gegenüber der Altheide deutlich erhöht.

Diskussion – Obwohl die erfolgreiche Etablierung von 89 kalkmagerrasentypischen Zielarten ein sorgfältiges und effizientes Vorgehen bei der Renaturierung belegen (EDWARDS et al. 2007, PYWELL et al. 2003), waren 21 Jahre nach Beginn der Maßnahmen noch deutliche Unterschiede zwischen der Vegetation der Renaturierungsflächen und der Kalkmagerasen im Naturschutzgebiet zu erkennen. Nur auf den Bodenabtragsflächen mit Einsaat seltener Arten unterschied sich die mittlere Zahl der Zielarten pro Plot nicht mehr signifikant vom Referenzzustand. Auf Flächen ohne Abtrag wurde deren Etablierung durch konkurrenzkräftige Grünlandarten beeinträchtigt, die kontinuierlich 20–30 % zur Bestandsdeckung beitrugen. Durch Obergräser wie *Arrhenatherum elatius* oder *Dactylis glomerata* war auch die Bestandshöhe signifikant erhöht, was die dortigen Etablierungsbedingungen für niedrigwüchsige konkurrenzschwache Arten erheblich beeinträchtigen kann (LEISHMAN 1999, VERHAGEN et al. 2001, FAGAN et al. 2008). Dies könnte auch erklären, warum von den fünf nachträglich in den Kontrollparzellen eingesäten Rote Liste-Arten nur eine, *Scabiosa canescens*, wiedergefunden werden konnte. Hinsichtlich der Artenzusammensetzung zeigte eine Ordination (DCA), dass die Vegetation der Parzellen mit Bodenabtrag auch die größte Ähnlichkeit zur Altheide aufwiesen. Die Vegetationsentwicklung in Richtung der Referenzflächen hat sich in den letzten Jahren allerdings sehr verlangsamt. Auf den Flächen, wo der feinkörnige Oberboden abgetragen wurde, liegt dies möglicherweise an den ungünstigen Entwicklungsbedingungen für die mesophytischen Arten der Kalkmagerrasen, die sich unter den extrem trockenen und nährstoffarmen Bedingungen anstehenden Kalkschotters kaum etablieren können. Die Einsaat von Arten der Roten Liste auf den Abtragsflächen war bei neun von 11 Arten erfolgreich. Bei etablierungsfreudigen Sippen wie *Pulsatilla patens*, *Globularia punctata* und *Centaurea triumfettii* überstiegen die Dichten auf den Abtragsflächen sogar deutlich die auf den Spenderflächen (vgl. RÖDER & KIEHL 2008). Anspruchsvollere Arten wie *Aster amellus* und *A. linosyris*, die sich auf den Abtragsflächen nicht etablierten, hätten dagegen möglicherweise eher von einer Einsaat auf Flächen ohne Bodenabtrag profitiert. Diese Artunterschiede zeigen, wie wichtig es ist, durch Kombination unterschiedlicher Renaturierungsvarianten ein breiteres Substratspektrum zu schaffen, um einen maximalen Etablierungserfolg zu erzielen (KAHMEN et al. 2002).

Eine Prognose der weiteren Vegetationsentwicklung ist schwierig. Zwar gab es auch auf den Kontrollflächen eine langsame Zunahme der Zielarten, die bisherigen Ergebnisse stehen aber im Gegensatz zu FAGAN et al. (2008), die auf lange etablierten Renaturierungsflächen mit direktem Anschluss an bestehende Magerrasen und ohne gezielte Renaturierungsmaßnahmen die größte Ähnlichkeit zu den Zielflächen beobachteten. Eine derartige Entwicklung ist auf den Kontrollflächen ohne Bodenabtrag und Mahdgut bislang nicht absehbar. Die Flächen mit Oberbodenabtrag werden sich aufgrund der extremen Standortbedingungen der skelettreichen Böden auch weiterhin von den ursprünglichen Magerrasen unterscheiden. Hier ist eher eine Entwicklung wie auf dem "Rollfeld“ zu erwarten, eine 1945 angelegten Bodenabtragsfläche im NSG Garchinger Heide, die sich durch ihre xerophytenreiche Vegetation noch heute deutlich von der Altheide unterscheidet (RÖDER et al. 2006). Auf den Flächen ohne Oberbodenabtrag halten sich hartnäckig Arten des produktiven Grünlandes, was in Anbetracht hoher P- und K-Gehalte im Boden (KIEHL et al. 2003) nach FAGAN et al. (2008) auch längerfristig so bleiben könnte.

Im vorgestellten Projekt haben die beteiligten Akteure das ursprünglich faktorielle Design nach zehn Jahren evaluiert und Flächen mit suboptimaler Entwicklung durch zusätzliche Mähgutübertragung und Aussaat von Rote Liste-Arten aufgewertet. Die Ergebnisse zeigen, dass ein solcher ‘dynamischer Renaturierungsansatz’, der flexibel auf Fehlentwicklungen reagiert, vielversprechende Möglichkeiten bietet, artenreiches Grünland mit hohem Naturschutzwert in einer überschaubaren Zeitspanne zu etablieren.

Author contributions

SH performed field work, analyzed the data and wrote the first draft of the manuscript. HA and TC supervised the research work, KK provided data and wrote parts of the manuscript and HA elaborated the final manuscript.

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Supplements

Supplement S1. Species constancies recorded in the following restoration treatments in 2014: without topsoil removal and hay transfer (control), without topsoil removal and with initial hay transfer (R^-M^e), with topsoil removal and initial hay transfer (R^+M^e), with topsoil removal and late hay transfer (R^+M^l).

Beilage S1. Stetigkeit der 2014 in den verschiedenen Behandlungsvarianten auf 4-m²-Probeflächen erfassten Gefäßpflanzenarten.

References

ABDI, H. (2007): Bonferroni and Sidak corrections for multiple comparisons. – In: SALKIND, N.J. (Ed.): Encyclopedia of measurement and statistics: 103–107. Sage, Thousand Oaks.

ALBRECHT, H. & AUERSWALD, K. (2009): Seed traits in arable weed seed banks and their relationship to land-use changes. – Basic Appl. Ecol. 10: 516–524.

BAKKER, J.P. & BERENDSE, F. (1999): Constraints in the restoration of ecological diversity in grassland and heathland communities. – Trends Ecol. Evol. 14: 63–68.

BAKKER, J.P., VAN DIGGELEN, R., BEKKER, R.M. & MARRS, R.H. (2012): Restoration of dry grasslands and heathlands. – In: VAN ANDEL, J. & ARONSON, J. (Eds.): Restoration Ecology: The New Frontier. 2nd ed.: 173–188. Blackwell Publishing, Oxford.

BAUER, M. & ALBRECHT, H. (2019): Vegetation monitoring in a 100-year-old calcareous grassland reserve in Germany. – Basic Appl. Ecol. 42: 15–26.

BAUER, M., KIEFER, J. & ALBRECHT, H. (2020): Vegetationsveränderungen auf Dauerbeobachtungsflächen im Naturschutzgebiet Garchinger Heide über 35 Jahre. – Mitt. Bayer. Bot. Ges. 90 (in print).

BEKKER, R.M., BAKKER, J.P., GRANDIN, U. … WILLEMS, J.H. (1998): Seed size, shape and vertical distribution in the soil: indicators for seed longevity. – Funct. Ecol. 12: 834–842.

BfN (Bundesamt für Naturschutz) (2018): Rote Liste gefährdeter Tiere, Pflanzen und Pilze Deutschlands: Band 7: Pflanzen. – Landwirtschaftsverlag, Münster: 784 pp.

CONRADI, T. & KOLLMANN, J. (2016): Species pools and environmental sorting control different aspects of plant diversity and functional trait composition in recovering grasslands. – J. Ecol. 104: 1314–1325.

DENGLER, J., JANIŠOVÁ, M., TÖRÖK, P. & WELLSTEIN, C. (2014): Biodiversity of palaearctic grasslands: a synthesis. – Agric. Ecosyst. Environ. 182: 1–14.

DIACON-BOLLI, J.C., EDWARDS, P.J., BUGMANN, H., SCHEIDEGGER, C. & WAGNER, H.H. (2013): Quantification of plant dispersal ability within and beyond a calcareous grassland. – J. Veg. Sci. 24: 1010–1019.

DONATH, T. & ECKSTEIN, L. (2010): Effects of bryophytes and grass litter on seedling emergence vary by vertical seed position and seed size. – Plant Ecol. 207: 257–268.

EDWARDS, A., MORTIMER, S.R., LAWSON, C.S. … BROWN, V.K. (2007): Hay strewing, brush harvesting of seed and soil disturbance as tools for the enhancement of botanical diversity in grasslands. – Biol. Conserv. 134: 372–382.

ENGST, K., BAASCH, A., ERFMEIER, A. … BRUELHEIDE, H. (2016): Functional community ecology meets restoration ecology: Assessing the restoration success of alluvial floodplain meadows with functional traits. – J. Appl. Ecol. 53: 751–764.

EUROPEAN COMMISSION (2007): Interpretation manual of European Union habitats: Version EUR 27. Brussels, European Commission DGXI. – URL: http://ec.europa.eu/environment/nature/legislation/habitatsdirective/docs/2007_07_im.pdf [accessed 2020–05–22].

FAGAN, K.C., PYWELL, R.F., BULLOCK, J.M. & MARRS, R.H. (2008): Do restored calcareous grasslands on former arable fields resemble ancient targets? The effect of time, methods and environment on outcomes. – J. Appl. Ecol. 45: 1293–1303.

FELLOWS, I. (2012): Deducer: a data analysis GUI for R. – J. Stat. Softw. 49: 1–15.

FETZER, K.D., GROTTENTHALER, W., HOFMANN, B. … WITTMANN, O. (1986): Standortkundliche Bodenkarte von Bayern 1:50.000. München-Augsburg und Umgebung. Erläuterungen. – Bayerisches Geologisches Landesamt, Munich: 396 pp.

FISCHER, M. & STÖCKLIN, J. (1997): Local extinctions of plants in remnants of extensively used calcareous grasslands 1950–1985. – Conserv. Biol. 11: 727–737.

GROSS, K.L. (1984): Effect of seed size and growth form on seedling establishment of six monocarpic perennial plants. – J. Ecol. 72: 369–387.

HARVOLK-SCHÖNING. S., OTTE, A., HARNISCH, M., MICHALSKA-HEJDUK, D. & DONATH, T.W. (2020): Floodplain meadow restoration revisited: Long-term success of large scale application of diaspore transfer with plant material in restoration practice. – Biol. Cons. 241: 108322.

HERVÉ, M. (2015): RVAideMemoire: Diverse basic statistical and graphical functions. – R package version 0.9-52.

HESLINGA, J.L. & GRESE, R.E. (2010): Assessing plant community changes over sixteen years of restoration in a remnant Michigan tallgrass prairie. – Am. Midl. Nat. 164: 322–336.

HILL, M.O. & GAUCH, H.G. (1980): Detrended Correspondence Analysis: An improved ordination technique. – Vegetatio 42: 47–58.

HIRST, R.A., PYWELL, R.F., MARRS, R.H. & PUTWAIN, P.D. (2005): The resilience of calcareous and mesotrophic grasslands following disturbance. – J. Appl. Ecol. 42: 498–506.

HÖLZEL, N. & OTTE, A. (2003): Restoration of a species-rich flood meadow by topsoil removal and diaspore transfer with plant material. – Appl. Veg. Sci. 6: 131–140.

HUBER, J. & KOLLMANN, J. (2019): Recruitment filtering by a moss layer disadvantages large-seeded grassland species. – Basic Appl. Ecol. 42: 27–34.

HUMMITZSCH, U. (2007): Langfristige Vegetationsentwicklung auf neu angelegten Kalkmagerrasen unter besonderer Berücksichtigung der Leguminosen und der Kryptogamen. – Master Thesis, TU Munich, Freising, Germany.

HUTCHINGS, M.J. & BOOTH, K.D. (1996): Studies on the feasibility of re-creating chalk grassland vegetation on ex-arable land. I. The potential roles of the seed bank and the seed rain. – J. Appl. Ecol. 33: 1171–1181.

JESCHKE, M. & KIEHL, K. (2006): Auswirkung von Renaturierungs- und Pflegemaßnahmen auf die Artendiversität von Gefäßpflanzen und Kryptogamen in neu angelegten Kalkmagerrasen. – Tuexenia 26: 223–242.

JESCHKE, M. & KIEHL, K. (2008): Effects of a dense moss layer on germination and establishment of vascular plants in newly created calcareous grasslands. – Flora 7: 557–566.

KAHMEN, S., POSCHLOD, P. & SCHREIBER, K.F. (2002): Conservation management of calcareous grasslands. Changes in plant species composition and response of functional traits during 25 years. – Biol. Conserv. 104: 319–328.

KIEHL, K. (2009): Langfristige Perspektiven für die Entwicklung neu angelegter Kalkmagerrasen in der Münchner Schotterebene. – Laufener Spezialbeiträge, Bayer. Akad. Naturschutz Landschaftspflege 2/09: 87–96.

KIEHL, K., KIRMER, A., DONATH, T.W., RASRAN, L. & HÖLZEL, N. (2010): Species introduction in restoration projects – Evaluation of different techniques for the establishment of semi-natural grasslands in Central and Northwestern Europe. – Basic Appl. Ecol. 11: 285–299.

KIEHL, K. & PFADENHAUER, J. (2007): Establishment and persistence of target species in newly created calcareous grasslands on former arable fields. – Plant Ecol. 189: 31–48.

KIEHL, K., THORMANN, A. & PFADENHAUER, J. (2003): Nährstoffdynamik und Phytomasseproduktion in neu angelegten Kalkmagerrasen auf ehemaligen Ackerflächen. – In: PFADENHAUER, J. & KIEHL, K. (Eds.): Renaturierung von Kalkmagerrasen. Angew. Landschaftsökol. 55: 39–71. Bundesamt für Naturschutz, Bonn-Bad Godesberg.

KIEHL, K., THORMANN, A. & PFADENHAUER, J. (2006): Evaluation of initial restoration measures during the restoration of calcareous grasslands on former arable fields. – Rest. Ecol. 14: 148–156.

KLEYER, M., BEKKER, R.M., KNEVEL, I.C. … PECO, B. (2008): The LEDA Traitbase: a database of life-history traits of the Northwest European flora. – J. Ecol. 96: 1266–1274.

KLOTZ, S., KÜHN, I. & DURKA, W. (Eds.) (2002): BIOLFLOR – Eine Datenbank zu biologisch-ökologischen Merkmalen zur Flora von Deutschland. – Schriftenr. Vegetationskd. 38: 1–334.

KRAUSS, J., BOMMARCO, R., GUARDIOLA, M. … STEFFAN-DEWENTER, I. (2010): Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels. – Ecol. Lett. 13: 597–605.

LALIBERTÉ, E., LEGENDRE, P. & SHIPLEY, B. (2014): FD: measuring functional diversity from multiple traits, and other tools for functional ecology. – R package version 1.0-12.

LAVOREL, S., GRIGULIS, K., MCINTYRE, S. … BONIS, A. (2008): Assessing functional diversity in the field – methodology matters! – Funct. Ecol. 22: 134–147.

LEISHMAN, M.R. (1999): How well do plant traits correlate with establishment ability? Evidence from a study of 16 calcareous grassland species. – New Phytol. 141: 487–496.

LEYER, I. & WESCHE, K. (2007): Multivariate Statistik in der Ökologie. – Springer, Berlin: 221 pp.

MATTHEWS, J.W. & SPYREAS, G. (2010): Convergence and divergence in plant community trajectories as a framework for monitoring wetland restoration progress. – J. Appl. Ecol. 47: 1128–1136.

MAURER, K., DURKA, W. & STÖCKLIN, J. (2003): Frequency of plant species in remnants of calcareous grassland and their dispersal and persistence characteristics. – Basic Appl. Ecol. 4: 307–316.

MOORE, D.S., MCCABE, G.B. & CRAIG, B.A. (2016): Introduction to the practice of statistics. – Freeman, New York: 814 pp.

OBERDORFER, E. (2001): Pflanzensoziologische Exkursionsflora, 8th ed. – Ulmer, Stuttgart: 1056 pp.
OBERDORFER, E. & KORNECK, D. (1976): *Festuco-Brometea*. – In: OBERDORFER, E. (Ed.) (1978): Süddeutsche Pflanzengesellschaften, Teil II: 86–182. Fischer, Jena.
OKSANEN, J., BLANCHET, F.G., KINDT, R. ... WAGNER, H. (2015): vegan: Community ecology package. – R package version 2.2-1.
PFADENHAUER, J. & KIEHL, K. (2003): Renaturierung von Kalkmagerrasen – ein Überblick. – Angew. Landschaftsökol. 55: 25–38. Bundesamt für Naturschutz, Bonn-Bad Godesberg.
PIQUERAY, J., BOTTIN, G., DELESCAILLE, L.M., BISTEAU, E., COLINET, G. & MAHY, G. (2011): Rapid restoration of a species-rich ecosystem assessed from soil and vegetation indicators: the case of calcareous grasslands restored from forest stands. – Ecol. Indic. 11: 724–733.
PIQUERAY, J., FERRONI, L., DELESCAILLE, L.M., SPERANZA, M., MAHY, G. & POSCHLOD, P. (2015): Response of plant functional traits during the restoration of calcareous grasslands from forest stands. – Ecol. Indic. 48: 408–416.
PÖLLINGER, A. & KIEFER, J. (2017): Gesamtartenliste Pflanzenarten der Garchinger Heide. – Unpublished report. Schober Gesellschaft für Landschaftsarchitektur mbH, Freising.
POSCHLOD, P. & WALLISDEVRIES, M.F. (2002): The historical and socioeconomic perspective of calcareous grasslands – lessons from the distant and recent past. – Biol. Conserv. 104: 361–376.
PYWELL, R.F., BULLOCK, J.M., ROYM, D.B., WARMANM, L.I.Z., WALKER, K.J. & ROTHERY, P. (2003): Plant traits as predictors of performance in ecological restoration. – J. Appl. Ecol. 40: 65–77.
R-CORE-TEAM (2014): R: A language and environment for statistical computing. – R Foundation for Statistical Computing, Vienna, Austria.
REICH, P.B., WALTERS, M.B. & ELLSWORTH, D.S. (1992): Leaf lifespan in relation to leaf, plant and stand characteristics among diverse ecosystems. – Ecol. Monogr. 62: 365–392.
RICO, Y., BOEHMER, H.J. & WAGNER, H.H. (2014): Effect of rotational shepherding on demographic and genetic connectivity of calcareous grassland plants. – Conserv. Biol. 28: 467–477.
RÖDER, D., JESCHKE, M. & KIEHL, K. (2006): Vegetation und Böden alter und junger Kalkmagerrasen im Naturschutzgebiet "Garchinger Heide" im Norden von München. – Forum Geobot. 2: 24–44.
RÖDER, D. & KIEHL, K. (2008): Vergleich des Zustandes junger und historisch alter Populationen von *Pulsatilla patens* (L.) Mill. in der Münchner Schotterebene. – Tuexenia 28: 121–132.
RYDGREN, K., HALVORSEN, R., TÖPPERM J.P. … SULAVIK, J. (2019): Advancing restoration ecology: A new approach to predict time to recovery. – J. Appl. Ecol. 56: 225–234.
SCHEUERER, M. & AHLMER, W. (2003): Rote Liste gefährdeter Gefäßpflanzen Bayerns mit regionalisierter Florenliste. – Schriftenr. Bayer. Landesamt Umweltschutz 165: 1–372.
SCHIEFER, J. (1984): Möglichkeiten der Aushagerung von nährstoffreichen Grünlandflächen. – Veröff. Naturschutz Landschaftspflege Baden-Württ. 57/58: 33–62.
SMITH, B.M., DIAZ, A. & WINDER, L. (2017): Grassland habitat restoration: lessons learnt from long term monitoring of Swanworth Quarry, UK, 1997–2014. – PeerJ 5: e3942.
TISCHEW, S., DIERSCHKE, H., SCHWABE, A. … HÄRDTLE, W. (2018): Pflanzengesellschaft des Jahres 2019: Die Glatthaferwiese. – Tuexenia 38: 287–295.
THOMPSON, K., BAKKER, J.P. & BEKKER, R.M. (1997): The soil seed banks of North West Europe. – Cambridge University Press, Cambridge: 276 pp.
THOMPSON, K., BAKKER, J.P., BEKKER, R.M. & HODGSON, J.G. (1998): Ecological correlates of seed persistence in soil in the north-west European flora. – J. Ecol. 86: 163–169.
TÖRÖK, P., VIDA, E., DEÁK, B., LENGYEL, S. & TÓTHMÉRÉSZ, B. (2011): Grassland restoration on former croplands in Europe: an assessment of applicability of techniques and costs. – Biodivers. Conserv. 20: 2311–2332.
VEEN, P., JEFFERSON, R., DE SMIDT, J., VAN DER STRAATEN, J. (Eds.) (2009): Grasslands in Europe of high nature value. – KNNV Publishing, Zeist: 320 pp.
VERHAGEN, R., KLOOKER, J., BAKKER, J.P. & VAN DIGGELEN, R. (2001): Restoration success of low-production plant communities on former agricultural soils after top-soil removal. – Appl. Veg. Sci. 4: 75–82.
VON BLANCKENHAGEN, B. & POSCHLOD, P. (2005): Restoration of calcareous grasslands: the role of the soil seed bank and seed dispersal for recolonisation processes. – Biotechnol. Agron. Soc. Environ. 9: 143–149.

WAGNER, H.H., RICO, Y., LEHNERT, H. & BOEHMER, H.J. (2013): Process-based long-term evaluation of an ecological network of calcareous grasslands connected by sheep herding. – Ecography 36: 374–382.

WALDÉN, E. & LINDBORG, R. (2016): Long term positive effect of grassland restoration on plant diversity – success or not? – PLOS ONE. 11:e0155836.

WEIHER, E., VAN DER WERF, A., THOMPSON, K., RODERICK, M., GARNIER, E. & ERIKSSON, O. (1999): Challenging Theophrastus: A common core list of plant traits for functional ecology. – J. Veg. Sci. 10: 609–620.

WESTOBY, M. (1998): A leaf-height-seed (LHS) plant ecology strategy scheme. – Plant Soil 199: 213–227.

WESTOBY, M., FALSTER, D.S., MOLES, A.T., VESK, P.A. & WRIGHT, I.J. (2002): Plant ecological strategies: Some leading dimensions of variation between species. – Annu. Rev. Ecol. Evol. Syst. 33: 125–159.

WILLEMS, J.H. (2001): Problems, approaches, and results in restoration of Dutch calcareous grassland during the last 30 years. – Restor. Ecol. 9: 147–154.

WILSON, J.B., PEET, R.K., DENGLER, J. & PARTEL, M. (2012): Plant species richness: the world records. – J. Veg. Sci. 23: 796–798.

WINDOLF, R. (1989): Geologie, Klima, Lebensbedingungen. – In: Gemeinde Eching (Ed.): Garchinger Heide, Echinger Lohe. Naturschutzgebiete in der Gemeinde Eching, Landkreis Freising: 13–25. Bruckmann, München.

WISSKIRCHEN, R. & HAEUPLER, H. (1998): Standardliste der Farn- und Blütenpflanzen Deutschlands. – Ulmer, Stuttgart: 764 pp.

WOODCOCK, B., MCDONALD, A. & PYWELL, R. (2011): Can long-term floodplain meadow recreation replicate species composition and functional characteristics of target grasslands? – J. Appl. Ecol. 48: 1070–1078.

Supplement S1. Species constancies recorded in the following restoration treatments in 2014: without topsoil removal and hay transfer (control), without topsoil removal and with initial hay transfer (R^-M^e), with topsoil removal and initial hay transfer (R^+M^e), with topsoil removal and late hay transfer (R^+M^l). The nature reserve Garchinger Heide was used as reference site. Constancy classes range from I (0 – 20%) to V (80 – 100%).

Beilage S1. Stetigkeit der 2014 in den verschiedenen Behandlungsvarianten auf 4-m²-Probeflächen erfassten Gefäßpflanzenarten. Stetigkeitsklassen von I (0 – 20%) bis V (80 – 100%). Behandlungsvarianten: ohne Bodenabtrag und Mähgut (control), ohne Bodenabtrag und mit sofortiger Mähgutübertragung (R^-M^e), mit Bodenabtrag und sofortiger Mähgutübertragung (R^+M^e), mit Bodenabtrag und späterer Mähgutübertragung (R^+M^l). Das Naturschutzgebiet Garchinger Heide diente als Referenzfläche.

	control	R^-M^e	R^+M^e	R^+M^l	nature reserve	SLA[a] [mm²/mg]	Canopy height [m]	Seed mass [mg]	SLI[b]	Dispersal type[c]				Species group[d]	Red List[e]
										aut	ane	zoo	hem		
Topsoil removal	no	no	yes	yes	no										
Hay transfer – initial	no	yes	yes	no	no										
Hay transfer – late	no	no	no	yes	no										
Additional sowing	yes	no	yes	yes	no										
Number of repetitions	12	8	5	6	8										
Mean no. of species (4m²)	28.7	32.8	26.4	21.9	32										
Mean no. of target-species (4m²)	15.6	23	24.4	18.5	30.1										
Target species which successfully established at sites with and without hay															
Linum perenne	V	V	III	IV	IV	25.9	0.65	2.2	0	yes	no	yes	yes	t	1
Genista tinctoria	III	V	V	V	II	18.1	0.45	3.57	0	yes	no	no	yes	t	-
Rhinanthus glacialis	V	V	III	III	V	NA	0.35	3.43	NA	no	no	yes	yes	t	-
Bromus erectus	V	V	III	II	V	17	0.5	4.49	0.1	no	no	yes	no	t	-
Festuca ovina agg.	III	V	IV	III	I	14.8	0.22	0.44	0.1	no	yes	yes	yes	t	-
Plantago media	V	V	II	.	II	19.3	0.04	0.39	0.29	yes	no	yes	yes	t	-
Silene nutans	IV	III	IV	V	.	22.2	0.18	0.32	0.33	yes	no	yes	yes	t	-
Centaurea scabiosa s.l.	II	V	IV	III	.	19.2	0.82	6.45	0.09	no	yes	yes	yes	t	-
Helianthemum nummularium	I	IV	V	IV	V	14.7	0.12	1.09	0.09	yes	no	yes	yes	t	-
Betonica officinalis	III	V	IV	I	IV	19.7	0.4	1.35	0.29	no	no	yes	yes	t	-
Koeleria pyramidata	II	V	II	III	II	16.5	0.32	2.3	0	no	yes	yes	yes	t	-
Peucedanum oreoselinum	I	IV	V	II	V	16.3	0.5	3.65	0	no	yes	yes	no	t	-
Galium verum agg.	I	IV	IV	III	.	20.8	0.42	0.51	0.03	yes	no	yes	yes	t	-
Arenaria serpyllifolia	V	III	II	.	.	19.4	0.16	0.07	0.65	no	no	yes	no	t	-
Prunella grandiflora	III	IV	V	.	II	20.1	0.18	0.86	0.18	yes	yes	yes	no	t	-
Centaurea jacea s.l.	II	III	V *	V *	V	16.4	0.85	1.99	0.1	yes	no	yes	yes	t	-
Pimpinella saxifraga	II	III	IV	I	III	15.8	0.41	1.15	0.01	yes	yes	yes	yes	t	-
Buphthalmum salicifolium	I	II	V	V	V	25.7	0.4	0.46	0.5	no	yes	no	yes	t	-
Asperula cynanchica	I	II	V	IV	V	28.1	0.18	0.96	0.21	no	no	yes	no	t	-
Filipendula vulgaris	III	V	I	.	V	18.4	0.35	0.79	0	no	yes	yes	no	t	3
Campanula rotundifolia agg.	I	II	V	II	.	24.1	0.19	0.06	0.36	yes	no	yes	yes	t	-
Medicago lupulina	V	V	I	I	.	27.2	0.38	1.78	0.35	no	yes	yes	yes	t	-
Senecio jacobaea	III	II	II	I	.	25.5	0.5	0.33	0.22	no	yes	yes	yes	t	-
Thymus praecox	I	I	V	III	IV	13.8	0.07	0.18	0.01	yes	yes	yes	no	t	-
Dianthus carthusianorum	II	II	III	.	.	16.4	0.26	1.03	0	yes	yes	yes	yes	t	-
Leontodon hispidus	II	I	I	III	IV	25.8	0.24	1.11	0.16	no	yes	yes	yes	t	-
Sanguisorba minor	I	I	I	III	.	20.5	0.2	4.24	0.09	no	yes	yes	yes	t	-
Linum catharticum	I	I	II	III	V	30.2	0.15	0.15	0.44	yes	yes	yes	yes	t	-
Arabis hirsuta	I	.	II	II	.	28.1	0.55	0.1	0.76	yes	no	yes	no	t	-
Galium boreale	.	I	I	II	II	19.4	0.42	0.71	0	no	no	yes	no	t	-
Potentilla neumanniana	I	.	I	I	.	12.5	0.1	NA	0.25	yes	no	yes	no	t	-
Species restricted to sites with initial hay transfer															
Seseli annuum	. *	I	IV	. *	.	NA	NA	NA	0	no	no	yes	no	t	3
Medicago falcata	.	I	I	.	.	18.1	0.35	1.64	0.08	no	no	yes	yes	t	-
Poa compressa	.	I	I	.	.	19.4	0.38	0.2	0.5	no	yes	yes	yes	t	-
Species mainly on sites with initial hay transfer															
Trifolium montanum	I	V	III	.	II	19.7	0.25	0.99	0.75	no	yes	yes	no	t	-
Brachypodium rupestre	I	V	I	I	V	22.8	0.6	3.02	0.04	no	yes	yes	no	t	-
Silene vulgaris	I	II	I	.	.	19.9	0.26	0.94	0.44	yes	no	yes	yes	t	-
Salvia pratensis	I	II	I	.	II	25.3	0.38	2.57	0.1	yes	yes	yes	yes	t	-
Species restricted to sites with topsoil removal															
Leontodon incanus	.	.	V	V	III	21.4	0.1	1.34	NA	no	yes	yes	no	t	-
Globularia punctata	.	.	IV *	V *	II	8.1	0.14	0.63	NA	yes	yes	no	no	t	3
Teucrium montanum	.	.	IV	V *	II	17.9	0.2	0.78	0	yes	no	yes	no	t	-
Centaurea triumfettii	.	.	V *	III *	.	NA	0.3	9.82	0	no	no	yes	no	t	1
Carex humilis	.	.	II	V	V	18.4	0.09	1.64	0	yes	yes	yes	no	t	-
Pulsatilla patens	. *	.	I	V *	III	NA	0.22	2.62	0	no	no	yes	no	t	1
Biscutella laevigata ssp. kerneri	. *	.	I	IV *	II	NA	0.15	3.61	0	no	yes	yes	no	t	3
Pseudolysimachion spicatum	.	.	III *	II *	.	10.1	0.21	0.12	0	no	no	no	yes	t	3
Euphrasia officinalis s.l.	.	.	II	III	III	17.3	0.24	0.13	0.17	no	yes	yes	no	ma	-
Carex ericetorum	.	.	II	III	III	NA	0.14	0.8	NA	yes	no	yes	no	t	3
Sedum acre	.	.	II	II	.	10.9	0.09	0.04	0.36	yes	yes	yes	yes	t	-
Betula pendula	.	.	I	I	.	17.9	25	0.19	0.75	no	yes	yes	yes	r	-
Globularia cordifolia	.	.	I	II	IV	NA	0.02	0.58	0.35	no	yes	no	no	t	-
Viola hirta	.	.	I	I	IV	18.2	0.08	3.09	0.59	yes	no	yes	no	t	-
Species mainly on sites with topsoil removal															
Scabiosa canescens	I *	I	III	V *	II	9.8	0.2	1.2	0	no	yes	yes	no	t	2
Hieracium piloselloides	I	.	V	III	.	26.8	0.11	0.32	NA	no	yes	yes	yes	t	-
Dorycnium germanicum	.	I	V	II	IV	NA	0.22	2.8	NA	no	no	no	no	t	3
Anthericum ramosum	.	I	V	IV	V	23.5	0.28	4.24	0	yes	no	yes	no	t	-
Anthyllis vulneraria	I	.	III	III	II	16.3	0.2	3.25	0.1	no	no	yes	yes	t	-
Hippocrepis comosa	I	.	V	II	IV	15.2	0.14	3.75	0.18	no	yes	yes	no	t	-
Calamagrostis epigejos	I	.	I	IV	.	13	1	0.08	0.14	no	no	yes	no	r	-
Hypericum perforatum	I	.	I	II	.	26.1	0.42	0.12	0.64	yes	yes	yes	yes	r	-
Chamaecytisus ratisbonensis	.	I	III	I	IV	NA	0.35	5.65	0	yes	no	yes	no	t	3
Scabiosa columbaria	I	I	I	I	I	19.2	0.28	1.95	0.16	yes	yes	yes	yes	t	-
Phleum phleoides	I	.	II	.	.	17.5	0.3	0.16	0.37	no	yes	yes	no	t	-
Species restricted to sites with topsoil removal and initial hay transfer															
Ononis spinosa agg.	.	.	II	.	.	28.4	0.28	4.95	0	yes	no	no	yes	t	-
Thesium linophyllon	.	.	I	.	IV	17.5	0.2	6.6	NA	no	no	yes	no	t	3
Verbascum densiflorum	.	.	I	.	.	17.1	1.38	0.1	NA	no	no	no	yes	r	-
Coronilla vaginalis	.	.	I	.	.	17.6	0.06	0.1	NA	no	yes	no	no	t	3
Carduus acanthoides	.	.	I	.	.	19	0.65	2.97	0.09	no	yes	yes	no	r	-
Conyza canadensis	.	.	I	.	.	22.4	0.52	0.05	0.5	no	yes	yes	yes	r	-
Oenothera biennis	.	.	I	.	.	15.7	1.18	0.58	0.55	yes	yes	yes	yes	r	-
Pulsatilla vulgaris s.l.	. *	.	I *	. *	II	10.1	0.15	3.26	0	no	yes	yes	yes	t	3
Sesleria albicans	.	.	I	.	.	20.7	0.15	0.9	0.2	no	yes	yes	yes	n/a	-
Species restricted to sites with topsoil removal and late hay transfer															
Potentilla heptaphylla	.	.	.	III	.	16	0.1	0.6	0	no	no	yes	no	t	-
Acer pseudoplatanus	.	.	.	II	.	16.7	25	69.2	0	no	yes	yes	yes	r	-
Potentilla cinerea ssp. incana	.	.	.	I	IV	13.3	0.08	NA	0.29	no	no	no	no	t	3
Polygala vulgaris s.l.	.	.	.	I	.	18.4	0.09	1.75	0.22	no	yes	yes	no	t	-
Prunus spinosa agg.	.	.	.	I	II	14.1	2	448.2	0	no	no	yes	yes	t	-
Odontites vulgaris	.	.	.	I	.	19.8	0.28	0.21	0.5	no	no	no	no	ma	-
Pinus sylvestris	.	.	.	I	.	5.3	40	7.57	0	no	no	no	no	r	-
Rubus spec.	.	.	.	I	.	24.7	1.3	95.7	0	yes	no	yes	no	r	-
Reseda lutea	.	.	.	I	I	17.9	0.28	0.68	0.9	no	no	yes	yes	r	-
Species missing on sites with topsoil removal															
Arrhenatherum elatius	V	V	.	.	.	28.3	1.27	3.08	0.06	yes	yes	yes	yes	ma	-
Trisetum flavescens	V	V	.	.	.	20.7	0.55	0.3	0.02	yes	yes	yes	yes	ma	-
Poa pratensis agg.	V	V	.	.	.	21.2	0.3	0.27	0.38	no	no	yes	yes	ma	-
Securigera varia	III	V	.	.	I	30.3	0.42	5.34	0.33	no	no	no	yes	t	-
Agrimonia eupatoria	III	III	.	.	.	18.4	0.25	14.18	0.02	no	no	yes	yes	t	-
Dactylis glomerata	IV	II	.	.	.	24.4	0.45	0.91	0.15	no	yes	yes	yes	ma	-
Trifolium pratense	IV	II	.	.	.	23.4	0.28	1.58	0.24	no	yes	yes	yes	ma	-
Tragopogon pratensis	III	II	.	.	.	19.1	0.35	10.34	0.12	no	yes	yes	yes	ma	-
Festuca pratensis	III	I	.	.	.	25.1	0.55	1.95	0.06	no	yes	yes	yes	ma	-
Veronica chamaedrys	III	III	.	.	.	31.6	0.25	0.21	0.42	yes	no	yes	no	ma	-
Festuca rubra agg.	II	II	.	.	.	19.4	0.48	0.91	0.14	no	yes	yes	yes	ma	-
Crepis biennis	II	I	.	.	.	31.2	0.57	1.31	0	no	yes	yes	yes	ma	-
Ranunculus bulbosus	II	II	.	.	.	18.1	0.18	2.87	0.36	no	yes	yes	no	t	-
Lathyrus tuberosus	.	II	.	.	.	29.7	0.65	33.39	0	yes	no	no	yes	r	-
Primula veris	I	II	.	.	.	18.7	0.1	0.8	0.05	yes	no	yes	yes	t	-
Veronica arvensis	I	I	.	.	.	25.7	0.14	0.12	0.34	no	yes	yes	yes	r	-
Inula hirta	.	II	.	.	.	21.2	0.28	0.22	0	no	yes	yes	no	t	3
Veronica austriaca	.	I	.	.	.	22.8	0.28	0.3	0	yes	no	yes	no	t	2
Salvia verticillata	.	I	.	.	.	15	0.3	0.89	0	yes	yes	yes	yes	t	-
Allium carinatum s.l.	.	I	.	.	I	28.3	0.22	1.29	NA	no	no	no	yes	t	3
Euphorbia verrucosa	.	I	.	.	V	NA	NA	NA	0.25	NA	NA	NA	NA	t	-
Knautia arvensis	I	I	.	.	.	19.7	0.42	4.13	0.05	no	no	yes	yes	ma	-
Campanula glomerata	.	I	.	.	.	24.4	0.38	0.14	0.5	yes	no	yes	yes	t	-
Orobanche gracilis	.	I	.	.	.	NA	NA	NA	NA	no	yes	no	no	n/a	-
Silene latifolia ssp. alba	I	I	.	.	.	21.6	0.48	0.96	0.45	yes	no	yes	yes	r	-
Vicia angustifolia	I	I	.	.	.	22.4	0.38	13.33	0.4	yes	no	no	yes	r	-
Vicia hirsuta	I	I	.	.	.	22.1	0.38	5.99	0.25	yes	no	yes	yes	r	-
Carum carvi	.	I	.	.	.	25.6	0.45	1.92	0	no	no	yes	yes	ma	-
Capsella bursa pastoris	.	I	.	.	.	30	0.14	0.1	0.91	no	yes	yes	yes	r	-
Helictotrichon pratense	.	I	.	.	.	10	0.65	2.68	0.06	yes	yes	yes	no	t	-
Species mainly on sites without hay transfer															
Daucus carota s.l.	II	I	.	I	.	19.6	0.52	1.16	0.31	no	no	yes	yes	ma	-
Helictotrichon pubescens	I	.	.	.	.	20.7	0.6	1.92	0.08	yes	yes	yes	no	t	-
Cirsium arvense	I	.	.	.	.	15.4	0.82	1.25	0.2	no	yes	yes	yes	r	-
Leucanthemum vulgare agg.	I	.	.	.	.	19.3	0.4	0.38	0.36	yes	no	yes	yes	ma	-
Origanum vulgare	I	.	.	.	.	24.7	0.38	0.1	0.41	yes	yes	yes	yes	t	-
Pastinaca sativa s.l.	I	.	.	.	.	32.9	0.45	3.9	0.29	no	yes	yes	yes	ma	-
Trifolium repens	I	.	.	.	.	31.4	0.2	0.59	0.38	no	no	yes	yes	ma	-
Cornus sanguinea	I	.	.	.	.	17.4	3	79.59	0.03	no	no	yes	no	r	-
Viola arvensis	I	.	.	.	.	24.3	0.12	0.47	0.86	yes	no	yes	yes	r	-
Erigeron annuus	I	.	.	.	.	28.1	0.68	NA	0.41	no	yes	yes	yes	r	-
Fragaria viridis	I	.	.	.	.	17	0.08	0.38	0.31	yes	no	yes	no	t	-
Polygonatum odoratum	I	.	.	.	II	32.9	0.3	264.3	0	yes	no	yes	yes	t	-
Species restricted to the nature reserve															
Euphorbia cyparissias	.	.	.	.	IV	22.6	0.22	1.96	0.19	yes	no	yes	yes	t	-
Briza media	.	.	.	.	III	21.6	0.16	0.4	0.02	no	yes	yes	yes	t	-
Danthonia decumbens	.	.	.	.	III	16.9	0.1	1.46	0.29	yes	no	yes	no	t	-
Carlina acaulis	.	.	.	.	II	11	0.31	4.08	0	no	yes	yes	yes	t	-
Daphne cneorum	.	.	.	.	II	NA	0.25	4.4	NA	no	no	yes	no	t	2
Erica carnea	.	.	.	.	II	NA	0.22	0.16	0.55	no	no	no	no	t	-
Polygala chamaebuxus	.	.	.	.	II	18.4	0.15	10	0	no	yes	yes	no	t	-
Potentilla alba	.	.	.	.	II	14.8	0.12	0.6	0	yes	no	yes	no	t	3
Hieracium pilosella	.	.	.	.	I	18.6	0.06	0.24	0.15	no	yes	yes	yes	n/a	-
Other species															
Lotus corniculatus agg.	V	V	III	IV	V	23.6	0.22	1.4	0.15	yes	no	yes	yes	ma	
Galium mollugo agg.	V	V	I	III	.	26.9	0.5	0.73	0.6	no	no	yes	yes	ma	
Achillea millefolium	V	III	I	I	.	18.9	0.48	0.13	0.1	yes	yes	yes	yes	ma	
Taraxacum officinale	V	III	I	I	I	29.5	0.2	0.66	0.26	no	yes	yes	yes	ma	
Cerastium holosteoides	IV	III	I	.	.	37.1	0.15	0.1	0.21	no	no	yes	yes	ma	
Trifolium campestre	III	IV	I	.	.	27.1	0.22	0.33	0.2	no	yes	yes	yes	r	
Plantago lanceolata	IV	II	.	I	.	18.5	0.15	1.62	0.24	yes	no	yes	yes	ma	
Picris hieracioides	IV	I	II	I	.	24.8	0.42	1.11	0.18	no	yes	no	no	r	
Clinopodium vulgare	II	I	.	I	.	23.6	0.42	0.43	0.44	yes	no	yes	yes	r	

* Red List species additionally sown between 2003 and 2013 (see Table 2).

a Specific Leaf Area [mm²/mg]

b Seed Longevity Index

c Seed dispersal type: aut: autochorous dispersal; ane: anemochorous dispersal; zoo: zoochorous dispersal; hem: hemerochorous dispersal

d Species group: t: target species (mainly of the class *Festuco-Brometea*); ma: species of productive grasslands (class *Molinio-Arrhenatheretea*); r: ruderals (arable weeds and ruderal species)

e Red List status in Bavaria (Ahlmer & Scheuerer 2003): 1: critically endangered; 2: endangered; 3: vulnerable