Tuexenia 44: 67–101. Göttingen 2024.
doi: 10.14471/2024.44.011, available online at www.tuexenia.de

Restoration of *Koelerion glaucae* vegetation in the Upper Rhine valley (Hesse, Germany): an update on the development of a model site after 19 years

Restitution von *Koelerion glaucae* Vegetation in der nördlichen Oberrheinebene (Hessen, Deutschland): aktualisierte Analyse der Entwicklung einer Modellfläche nach 19 Jahren

Christian Storm[1], Michael Stroh[2] & Angelika Schwabe[3 *]

[1]Technical University Darmstadt, Department of Biology, Chemical Plant Ecology, Schnittspahnstr. 10, 64287 Darmstadt, Germany; [2]Bahnstr. 16, 63303 Dreieich, Germany; [3]Technical University Darmstadt, Department of Biology, Schnittspahnstr. 10, 64287 Darmstadt, Germany
**Corresponding author, e-mail: schwabe@bio.tu-darmstadt.de*

Abstract

We present an update on our studies on the restoration of the highly endangered *Koelerion glaucae* vegetation in the Upper Rhine valley (Hesse, Germany), a habitat type protected by the European Union Fauna-Flora-Habitat directive. Our three-step restoration approach (deep-sand deposition, inoculation with plant material, non-intensive donkey grazing) was previously introduced after 10 years in this journal. Subsequently, the experiment was expanded, enabling the analysis of the permanent plots of the older restoration site (19 years) but also those of a younger "neodune" (15 years). Phytosociological relevés were sampled for nine permanent plots in a nested approach, with two sizes (25 and 79 m²; both circular), and the data were analyzed using a constancy table, ordination, classification, and the calculation of structural and diversity variables, including the target-species ratio (= TSR, qualitative and quantitative).

Our results show that the development commenced with a *Stellarietea* stage which was replaced after 3 years by a stage dominated by target species (*Koelerio-Corynephoretea*, *Festuco-Brometea*). The phytodiversity reached its peak after 5–11 years, while the vegetation cover steadily increased. In recent years, the rate of development has slowed and reached a relatively stable state; slight changes are indicated by the occurrence of *Festuco-Brometea* species and an increase in bryophytes. A comparison of the older (R) and younger (Y) restoration plots revealed striking similarities, reinforcing the broad applicability of the approach. Remarkably, the initial floristic composition (modulated by diaspores from the donor sites) has not been fully equalized even after 19 years. The applied plot sizes revealed that the smaller plots captured fewer species (later years: ca. 80–90%) and that the larger plots reduced the effects of stochastic processes. As expected, the TSR was scarcely affected by plot size. The impact of heat/drought years on the annuals was found to be very limited, in contrast to the more exposed "Griesheimer Sand" near Darmstadt.

The results demonstrate that after 19 years, the *Koelerion glaucae* vegetation exhibited excellent development. The TSR_{qual} reached its peak at the end of the study period, whereas TSR_{quant} and the number of red-listed/near-threatened species achieved a high level earlier. All values attained the benchmark established by the reference sites. In conclusion, the success of the restoration project was

Manuscript received 13 July 2024, accepted 12 November 2024
Published online 23 December 2024
Co-ordinating Editor: Annette Otte

exceptionally high, and the project could serve as a model for the restoration of this vanishing habitat type. The management by donkey grazing is necessary to maintain the diverse pattern of mainly *Koelerion glaucae* vegetation and secure the restoration.

Keywords: *Alyssum gmelinii*, *Bassia laniflora*, deep-sand deposition, donkey grazing, *Koeleria glauca*, inoculation of plant material, *Poa badensis*, red-listed species, restoration ecology, target species

Erweiterte deutsche Zusammenfassung am Ende des Artikels

1. Introduction

In the whole EU, dry calcareous steppic inland sand vegetation belongs to extremely endangered habitat types, and this is especially true for the pioneer stages (in Germany: *Jurineo cyanoidis-Koelerietum glaucae* Volk 1931, belonging to the alliance *Koelerion glaucae* Volk 1931). The habitat type is listed as endangered in the Fauna-Flora-Habitat directive (FFH) with Code 6120 as "Xeric sand calcareous grasslands (*Koelerion glaucae*)" (European Commission 2013). *Koelerion glaucae* vegetation is rich in endangered plant species (*Alyssum gmelinii*, *Bassia laniflora*, *Koeleria glauca*, and *Poa badensis*, among others) and also in xerophilous endangered animal species of different taxonomic groups (Ssymank et al. 1998, Beil et al. 2014; see examples in Figs. 1a–c). In the case of the restoration project of this study, donkey grazing was applied to manage the *Koelerion glaucae* habitat type (Fig. 1d).

In the northern Upper Rhine valley in Hesse, only remnants of this type existed in the 1990s in a few protected areas, mainly scattered in a fragmented landscape. Meanwhile, the situation has been substantially improved by grazing management (sheep, donkeys) of the existing areas as well as by restoration approaches combined with grazing in new areas, which are partly connected with older ones and form connectivity corridors in the landscape (Storm et al. 2016, 2022). Nevertheless, the covered area is still much smaller today than in the midst of the 20th century and far smaller than in the Middle Ages (Schwabe et al. 2024). Enlargement of settlements, agricultural use, afforestation, a decrease in sand dynamics in the small sites, the invasion of generalists/neophytes, eutrophication, and grass encroachment/ruderalization (the last process often combined with spontaneous succession) are the main reasons for the severe decline. Declines and species changes have also been shown for different types of endangered sandy vegetation across Europe (e.g., Kooijman & van der Meulen 1996, Wiesbauer et al. 1997, Riksen et al. 2006, Ketner-Oostra et al. 2012, Kollmann 2019) and this is also true for many grasslands in Europe with low-competitive species (e.g., Timmermann et al. 2015, Klinkovská et al. 2024).

Restoration approaches in nutrient-poor grasslands have been very successful in the last about 20 years, especially if the following problems could be solved: 1) reduction of high soil nutrient levels, e.g., by topsoil removal (Hölzel & Otte 2003, Gilhaus et al. 2015) or use of substrate with nutrient-poor conditions (this experiment: first publication Eichberg et al. 2010); 2) increase of the availability of diaspores (especially of target species) with different techniques (review of Kiehl et al. 2010); 3) management, especially to suppress competitive tall-growing plant species (e.g., by grazing: Körner et al. 2018) and create gaps for low-competitive ones.

In general, a very difficult task is to preserve *Koelerion glaucae* vegetation for longer time periods because the vegetation type is part of a dynamic system. Therefore, there are only very few sites in our area that persisted for longer than 30 years. Even by combined

Fig. 1. a) There are still high population numbers of the *Koelerion glaucae* species *Alyssum gmelinii* on the studied restoration site (corridor); to the left: leaves of *Helianthemum nummularium* subsp. *obscurum* (07.04.2024). **b)** Very open part of the corridor with fruiting *Koeleria glauca* and one of the typical xerophilous insect species which colonized the corridor: the endangered sphecid wasp *Bembix rostrata* (Spheciformes). Inset picture, arrow: *Bembix* between the shadows of the *K. glauca* culms with the microsite of a breeding cell and enlarged view of the insect (17.06.2015). **c)** Fruiting aspect of *Bassia laniflora* on the studied restoration site (see for the seedling aspect in early May: Storm et al. 2016, Fig. 7) (27.09.2015). **d)** Donkey grazing on the older and to the left the newer parts of the corridor. Donkeys prefer ruderal species but also feed, e.g., on *Artemisia campestris*. View to the north (27.09.2024) (All photos: A. Schwabe).

Abb. 1. a) Auf der untersuchten Restitutionsfläche (Korridor) gibt es noch große Populationen der *Koelerion glaucae*-Art *Alyssum gmelinii*; links: Blätter von *Helianthemum nummularium* subsp. *obscurum* (07.04.2024). **b)** Sehr offener Teil des Korridors mit fruchtender *Koeleria glauca* und einer der typischen thermophilen Insektenarten, die den Korridor kolonisiert haben: die gefährdete Grabwespe *Bembix rostrata* (Spheciformes). Pfeil: *Bembix* zwischen den Schatten der *K. glauca*-Halme mit dem Brutzellen-Mikrohabitat. Ausschnittbild: vergrößertes Bild von *Bembix* (17.06.2015). **c)** Fruchtaspekt von *Bassia laniflora* auf der untersuchten Restitutionsfläche (siehe zum Keimpflanzen-Aspekt im frühen Mai: Storm et al. 2016, Fig. 7) (27.09.2015). **d)** Eselbeweidung auf den älteren Bereichen und links der neueren Erweiterung des Korridors. Esel präferieren Ruderalarten, fressen aber auch z. B. *Artemisia campestris*. Blick nach Norden (27.09.2024) (Alle Fotos: A. Schwabe).

donkey and sheep grazing for about 20 years, it was not possible to restore *Koelerion glaucae* vegetation in one of the most valuable nature protection sites of calcareous sand vegetation in Hesse ("Griesheimer Düne und Eichwäldchen"): the cover decreased from 2.2 ha in 1983 to only 300 m^2 in 2023 (Schwabe et al. 2024). Meanwhile, the small populations of *K. glauca* have low flowering and fruiting success in this area.

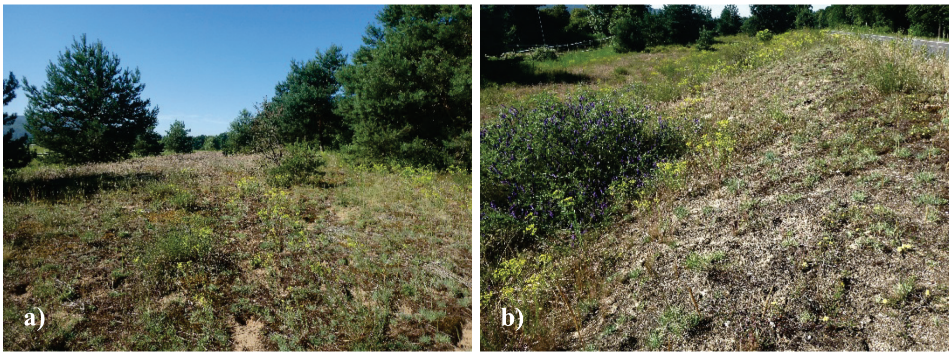


Fig. 2. a) Central part of the corridor, 20 years after deep-sand deposition and regular donkey grazing management (R plots) with *Koeleria glauca* and *Euphorbia seguieriana* aspect. The vegetation still has a gappy structure. View to the south. **b)** Newer part of the corridor, 16 years after sand deposition (Y plots), on the right side (left side: older parts). In the foreground: *Koeleria glauca* and flowering *Fumana procumbens*. Mainly on the older parts: flowering *Euphorbia seguieriana*. View to the south (both photos: A. Schwabe, 08.06.2024).

Abb. 2. a) Zentraler Teil des Korridors, 20 Jahre nach der Tiefensand-Aufschüttung und regelmäßiger Eselbeweidung (R-Plots) mit *Koeleria glauca* und *Euphorbia seguieriana*-Aspekt. Die Vegetation hat immer noch eine lückige Struktur. Blick nach Süden. **b)** Neuerer Teil des Korridors, 16 Jahre nach der Sandaufschüttung (Y-Plots) auf der rechten Seite (linke Seite: ältere Teile). Im Vordergrund: *Koeleria glauca* und blühende *Fumana procumbens*. Vor allem auf dem älteren Korridor: blühende *Euphorbia seguieriana*. Blick nach Süden (beide Fotos: A. Schwabe, 08.06.2024).

To explore the possibilities of a complete induced restoration of *Koelerion glaucae* vegetation (beginning with juvenile calcareous sand), we started a field experiment in 2005 with a three-step restoration approach of deep-sand deposition, inoculation with plant material rich in diaspores from well-developed donor sites, and non-intensive grazing. We reported about the first 4 years of the vegetation development (Eichberg et al. 2010, and about the first 10 years (Storm et al. 2016). In 2023, the experiment had been running for 19 years (Fig. 2a). In 2008, the restoration site was enlarged (Fig. 2b). In the two publications, we introduced the study site and the applied methods, so we mention only the essential aspects here. We sampled phytosociological relevés with two different plot sizes (25 m^2 and 79 m^2) each year, including all vascular plant species as well as bryophytes and lichens.

A global review of papers about restoration of open ecosystems (2011 to 2021) shows that the mean study period of restoration projects (active restoration) was 8.6 years (standard deviation ± 7.8) and sampling was carried out mostly at a low frequency (Barbosa-Dias et al. 2024). Therefore our project with annual sampling for 19 years should provide valuable data to evaluate the long-term success of *Koelerion glaucae* restoration.

Transfer of plant material (containing generative and vegetative diaspores of vascular plant species as well as thallus fragments of lichens and bryophytes) due to diaspore limitation is a frequently applied method in restoration practice (e.g., Hölzel et al. 2012, Kollmann 2019, Durbecq et al. 2022), but there is a lack of knowledge, especially concerning *Koelerion glaucae* vegetation. We used an approach with mown and raked plant material of well-developed target areas (Eichberg et al. 2010) and compared the results of the restoration site with the donor sites, which also served as reference sites to assess restoration success (e.g., Hölzel et al. 2012).

In the long run, the development of a mosaic of pioneer stages (*Koelerion glaucae*) and (to a lesser extent) more consolidated stages (*Allio sphaerocephali-Stipetum capillatae* Korneck 1974) and the suppression of tall-growing ruderal species should be maintained by restorative grazing dynamics by donkeys.

All developments in the 19-year time axis were superimposed by years with extreme heat and/or drought periods. The potential impact of these events, which may increase in the future, will be discussed in the context of the restoration experiment.

We asked the following questions: (1) Was there a continuous development of red-listed/near-threatened plant species and target species in general? (2) Was there a successful establishment and development of the endangered pioneer stages of subcontinental calcareous sand vegetation (*Koelerion glaucae*) as well as to a lesser extent more consolidated stages and how can the development be described over the extended period of 19 years? (3) Can we use the target-species ratio (TSR) as a synoptic value for different plot sizes, also compared with other pioneer and grassland vegetation types? (4) Was there an impact of extreme heat/drought years which affected the species structure?

2. Material and methods

2.1 Sandy area in the northern Upper Rhine valley (Hesse)

As already described by Storm et al. (2016), calcareous sands from the Rhine terraces were blown out in late glacial and early post-glacial times in the northern Upper Rhine valley. In a biogeographical transition zone between subcontinental, subatlantic, and submediterranean conditions, plant species of these different regions still characterize the remnant areas, which today are mostly situated in protected sites. The (for the climate conditions in Germany) relatively high annual average temperatures as well as low annual precipitation (1981–2010: 10.5 °C, 658 mm a^{-1}; 2004–2020: 11.3 °C; Frankfurt International Airport, Deutscher Wetterdienst, www.dwd.de) were strengthened in the investigation period by years with drought and heat (especially 2011, 2015, 2018, and 2022; see Schwabe et al. 2024). This will be shown in detail in Section 3.5.

2.2 Restoration experiment and fieldwork

For the field experiment near Seeheim-Jugenheim (10 km south of Darmstadt) on an ex-arable field, we constructed in 2005 a sand corridor (250 m × 22 m) between a small nature reserve with *Koelerion glaucae* and *Allio-Stipetum* vegetation and an older restoration site (Fig. 3). In the following sections, this restoration site will be referred to as the “corridor”.

In a three-step approach, we made the following interventions. (1) The topsoil of the ex-arable field was not removed. We deposited calcareous sand from deep soil layers of construction sites to a height of 1.5–3 m on top of the ex-arable field. The concentrations of plant-available nutrients (phosphate, nitrate, and ammonium) in the new substrate were low (for values in 2005, see Suppl. E1 in Storm et al. 2016). (2) Directly afterwards, we inoculated the bare sand with raked/mown plant material from two donor sites (S: *Koelerion glaucae/Allio-Stipetum* complex and T: pioneer vegetation with *Corynephorus canescens, Phleum arenarium*, and *Koelerion glaucae* vegetation); for the weights of the inoculated phytomass, see Eichberg et al. (2010), Storm et al. (2016). (3) Since autumn 2006, donkey grazing with low intensity was established for about 3 weeks each year, and since 2020 every 2nd year. Manual management was applied against woody species, especially *Robinia pseudoacacia* and *Ailanthus altissima,* and punctually for the invasive graminoid *Cynodon dactylon*. Due to the great importance of the endangered butterfly species *Lysandra bellargus* (occurring in the wider area), *Hippocrepis comosa* (the specific food plant of the caterpillar) was inoculated at the beginning of the experiment in 2006 by seeds and established itself. Since 2008, *L. bellargus* colonized the corridor (Ernst 2017).

Fig. 3. Restoration area (orientation northward) with the plots of the older corridor (R1–R6) and the younger enlargement (Y1–Y3). In the north: nature reserve with reference area and donor site with the S plots. The T reference area and donor site is located 8 km to the north in the same natural spatial unit. At the bottom of the picture (green area in the southwest): restoration site from 1998 (Stroh et al. 2002, 2007). Aerial photo: 'Hessische Verwaltung für Bodenmanagement und Geoinformation' in cooperation with "Landkreis Darmstadt-Dieburg"; 12.08.2012.

Abb. 3. Restitutionsfläche (nach N orientiert) mit den Plots des älteren Korridors (R1–R6) und der jüngeren Erweiterung (Y1–Y3). Im Norden: Naturdenkmal mit Referenz- und Spenderfläche mit den S-Plots. Die T Referenz- und Spenderfläche befindet sich 8 km nördlich in derselben naturräumlichen Einheit. Unten im Bild (grüne Fläche im Südwesten): Restitutionsfläche von 1998 (Stroh et al. 2002, 2007). Luftbild: „Hessische Verwaltung für Bodenmanagement und Geoinformation" in Kooperation mit dem „Landkreis Darmstadt-Dieburg"; 12.08.2012.

Until now, there was only initial soil development in the *Koelerion glaucae* vegetation with very low humus content, which is the first step in the development of the soil type "Locker-Syrosem" according to the German soil classification (AG Boden 2005), which corresponds to Calcaric Arenosol (Zech et al. 2022) in the international classification.

From 2005 until 2023, we yearly sampled the six 25 m^2 plots of the restoration site (R1–R6; Fig. 3) and, additionally, enlarged plots of 79 m^2 (both circular, nested approach). The plots were placed systematically (equidistant) along the corridor to ensure representation of the full extension. All plots were established in the center of each cross section to minimize edge effects. We used the Braun-Blanquet scale for the 25 m^2 plots (Storm et al. 2016) and for the 79 m^2 plots additionally a percentage scale. The larger plots were not analyzed in the previous studies by Eichberg et al. (2010) and Storm et al. (2016).

The southern part of the corridor, with the plots R1–R3, was inoculated by material from donor site T (open former military area dominated by pioneer stages with *Koelerion glaucae* vegetation, 8 kilometers north of the corridor in the same natural spatial unit), and the northern part, with the plots R4–R6, by plant material from donor site S (with a mosaic of *Koelerion glaucae* and *Allio-Stipetum* vegetation in the direct vicinity of the corridor).

Further, there are relevés, with a size of 25 m^2 (rectangular), from the donor sites T and S from different years (only one S plot with *Jurinea cyanoides* has a size of 10 m^2 due to the small-scale pattern of this community). Only for the T plots are there also circular 79 m^2 relevés.

In 2008, the corridor was enlarged after cutting *Populus* x *canadensis* trees in autumn 2008, and three new permanent plots of 25 m^2 and 79 m^2 could be sampled yearly from 2009 to 2023 (Y1–Y3; Y = younger restoration plots; Fig. 3). Plot selection and field work was identical to the R plots. The enlarged part has the structure of a neodune, with eastern exposure and a slope of mostly about 15° toward the old corridor of the restoration site. The new site was inoculated in November 2008 only by raked plant material from donor site S (*Koelerion glaucae* core area) and from pioneer vegetation with *Bassia laniflora* (Darmstadt-Eberstadt, "Düne am Ulvenberg"). One aim was to establish the endangered *B. laniflora* permanently; therefore, autumn was a suitable time window, with fruiting *Bassia* specimens still present and *Bassia* seeds near the mother plants (typical for this plant species; see Schwabe et al. 2000 for the donor site Darmstadt-Eberstadt). The C4 plant *B. laniflora* is no seed-bank species and needs higher temperatures for germination; therefore, germination is usually in May in our region. Fluctuations are high (Schwabe et al. 2000). In 2024, hundreds of seedlings developed on the corridor in a warm spring period at the beginning of April, always in the vicinity of the parental plants.

2.3 Multivariate analyses

The ordination of vegetation data was conducted by detrended correspondence analysis (DCA, Leyer & Wesche 2007). We present the ordination of the relevés at the 25 m^2 plots with the Braun-Blanquet scale because (1) this allows better comparability with the previous publications and (2) the plot sizes of the restoration and target plots are largely equal. The diagram with the 79 m^2 plots is presented in the electronic appendix (Supplements E1; see Section 3.3). The Braun-Blanquet data were previously rank-transformed. Rare species were downweighted, and axes were rescaled by 26 segments. Coefficients of determination between Sørensen distances in the ordination space and the original space were determined as a post hoc evaluation of ordination efficiency, representing the explained variance of each ordination axis. Graphical overlays of various structural and diversity variables (see below) have also been created. The variables are represented as vectors in the ordination diagram if their r^2 values with the ordination axes exceeded 0.3.

As an alternative to DCA, we performed a nonmetric multidimensional scaling ordination (NMDS), which resulted in a three-dimensional solution with final stress = 9.8 and final instability = 0.037. The axes were rotated to principal axes. The resulting graphs were very similar to those obtained by DCA. However, the NMDS presented some aspects in a misleading way (e.g., too close relationships between restoration and donor plots in the graph of ordination axes 1 and 2). For this reason, and to ensure comparability with our last publication, we present here only the results of the DCA. In a review article, Von Wehrden et al. (2009) pointed out problems of NMDS with certain data sets and a lack of verification, which also explains why there is still a "pluralism and diversity of ordination methods" in multivariate analyses. The usefulness of DCA for certain applications was also confirmed in a more recent comparison (Wildi 2018).

Additionally, a cluster analysis of the same data set was performed using the flexible beta classification method (beta = -0.5) and Sørensen distances. Mean Sørensen distances were also calculated between restoration plots and reference plots using presence-absence data. The significance of differences was determined by paired sample *t*-tests. The software utilized for the multivariate analyses was PC-ORD 7.11 (Wild Blueberry Media LLC, Corvallis, OR, USA).

2.4 Structural and diversity variables

In order to assess the success of the restoration project, it is necessary to define the target species. As the objective of this study was the restoration of dry sandy pioneer and grassland vegetation, the species of the *Koelerio-Corynephoretea* or *Festuco-Brometea* classes and those considered overarching are regarded as target species. The assignments were made using Oberdorfer (2001) as well as the main occurrences in target communities at the local scale level.

Target-species ratios offer a useful metric for measuring the contribution of target species to vegetation composition and therefore provide an appropriate indicator of restoration success (Eichberg et al. 2010). The qualitative target-species ratio (TSR_{qual}) is defined as the number of target plant species divided by the total number of plant species. The quantitative target-species ratio (TSR_{quant}) is calculated as the sum of the cover of target plant species divided by the sum of the cover percentages of all plant species.

The species numbers, sums of the cover percentages of species, and TSR values were calculated on the basis of the 79 m² plots, as these represent the species more completely (see Section 3) and were recorded with a percentage scale. As such data were not available from reference site S, the smaller plot sizes had to be used in that case, and the Braun-Blanquet data were transformed according to the following conversions: r = 0.1%, + = 0.3%, 1 = 1%, 2m = 3%, 2a = 9%, 2b = 19%, 3 = 38%, 4 = 63%, 5 = 88%. In order to facilitate comparison of plot types, we provided mean values ± standard errors in all cases.

2.5 Nomenclature and references for red-listed species

The categorization of red-listed species refers to the lists for Germany from Metzing et al. (2018) for vascular plant species, Caspari et al. (2018) for bryophytes, and Wirth et al. (2011) for lichens. The nomenclature of vascular plant species is based on Jäger (2017), that of bryophytes on Caspari et al. (2018), and that of lichens on Wirth et al. (2011). We included near-threatened species in our analyses.

3. Results

3.1 Floristic structure in the time axis shown in a constancy table of the restoration site

The constancy table (Supplement S1) shows the data of the 79 m² plots of the older restoration site (R1–R6; 19 years) and that of the plots of the younger site (Y1–3; 15 years) in the time axis.

In the course of the development, the **open soil** decreased from 99% to 40–50% in the 9th year to under 20% since the 15th year at the R as well as Y plots. These values still exceed those of the reference sites, with S at 10% and T at 13%.

In the open sand habitat of the 1st year, the **species numbers of *Koelerio-Corynephoretea* species** were still low (all in all: eight in the R plots) versus 18 *Stellarietea* species. Already in the 2nd year until the 19th year, about 20 *Koelerio-Corynephoretea* species/year were present in all R plots. In the last years, there was a tendency of decreasing species numbers. *Stellarietea* species decreased mainly in the 4th to 7th year (about five and fewer: R plots). Similarly, *Artemisietea* und *Molinio-Arrhenatheretea* species decreased nearly completely (with the exception of *Cerastium holosteoides*) in the R plots (from about the 6th to 10th year). In October of the 2nd year, donkey management started with high grazing preference, first on the ruderal species and later on, for example, *Artemisia campestris*.

The **floristic structure of *Koelerion glaucae* vegetation** of the R plots with *Koeleria glauca*, *Alyssum gmelinii*, and the pioneer species *Silene conica* and *Phleum arenarium* reached 100% constancy for many years, including the last year, and 30% to 50% constancy in the case of *Poa badensis* and *Bassia laniflora* in the last years. All these species were also present with similar constancy values in the Y plots. *Jurinea cyanoides* established itself in one Y plot in the 2nd year, but it persisted only for 5 years. The *Corynephoretalia* species *Thymus serpyllum* and *Corynephorus canescens* established themselves in most of the R plots and in all Y plots. *Euphorbia seguieriana* showed excellent vitality in the *Koelerion glaucae* vegetation of the corridor (see Section 4.1 for the supraregional phytosociological affiliation). The species is present in all R and Y plots, is avoided by donkeys, and therefore benefits from this management. *Fumana procumbens* (with regional occurrences also in *Koelerion glaucae* vegetation) also shows high vitality and established itself since the 2nd year of sampling (parts of the R and Y plots); see Section 4.1 for the supraregional phytosociological affiliation. There were scarcely successful establishments of **species of *Allio sphaerocephali-Stipetum capillatae* Korneck 1974 (*Festuco-Brometea*)**, which are able to dominate higher developed sand vegetation, such as *Stipa capillata* and *Koeleria macrantha.* Both species established themselves in the R plots (one to two plots) but vanished after 11 to 12 years; *S. capillata* also developed in one Y plot. Only *Phleum phleoides* was a successful graminoid species with a high presence in the R plots (but with a cover of at most 5%); additionally, other ***Festuco-Brometea* species**, such as *Asperula cynanchica*, occurred and showed some successional development.

The **bryophyte vegetation** was mainly characterized by the acrocarpic pioneer moss *Syntrichia ruralis* var. *ruraliformis*, which occurred in all R plots and had from the 13th year an average cover in the R plots of between 30% and 49% (Supplement S1). Especially from the 17th year, this species showed high average cover values of nearly 50% in the R plots. The pleurocarpic species *Hypnum cupressiforme* var. *lacunosum* and *Brachythecium albicans* showed in the last 9 years also a presence of 100% (R plots) or lower (Y plots). The average cover of *H. cupressiforme* var. *lacunosum* adds up to between 11% and 23% from the 13th year at the R plots. In one plot (R4), *H. cupressiforme* var. *lacunosum* already covered 60% to 70% in the last years.

Remarkable is the **development of the ruderal and often monodominant species *Calamagrostis epigejos*** in the course of the 19 years. In the middle of the time period, after the 7th year, *C. epigejos* was present in all six R plots; afterward it strongly decreased. The cover was 4–5% between the 10th and 12th year; in earlier and later years, it was only <1% (R plots, average values p. a.). In the Y plots, there was a similar development; the species even vanished completely in the last year.

3.2 Comparison of the floristic structure of target species: donor and restoration sites

The six plots of the donor sites T (pioneer stages, *Koelerion glaucae*) and S (*Koelerion glaucae* and *Allio sphaerocephali-Stipetum capillatae*) were characterized by the occurrence of 47 target vascular plant species (T: 22; S: 40). The open T site had large populations of *Corynephorus canescens* and *Phleum arenarium* (not on site S), which were successfully transferred and established themselves on the restoration site. Only seven species never occurred on the corridor, mostly *Festuco-Brometea* species from site S, showing higher developed successional stages (*Bromus erectus*, *Centaurea scabiosa*, *Medicago falcata/M. x varia*, *Potentilla cinerea* subsp. *incana*, *Sanguisorba minor*, *Scabiosa canescens*), and one *Koelerio-Corynephoretea* species from site T: *Poa bulbosa* (a species with frequent fluctuations). Therefore, 85% of all target species established themselves on the restoration site. On the other hand, 11 target species could be detected on the corridor that are not represented in the relevés of the donor plots, from which four species were present only in the first years (*Acinos arvensis*, *Medicago lupulina*, *Ranunculus bulbosus*, *Erodium cicutarium*). *Bassia laniflora* and *Hippocrepis comosa* were introduced by additional inoculation measures (see Section 2.2). The steppe species *Bassia laniflora* colonized one to two Y plots and one to three R plots in the last 15 years and one Y plot and three R plots in 2023. The seed-bank species *Rumex acetosella*, *Sedum acre,* and *Trifolium arvense*, as well as the wind-dispersed *Vulpia myuros*, colonized the corridor spontaneously. The rare species *Orobanche arenaria* (a parasite mostly of *Artemisia campestris*) also established itself spontaneously.

3.3 Multivariate analyses

A detrended correspondence analysis (DCA) on the relevé data (including bryophytes and lichens) from the 25 m² plots was conducted. The after-the-fact assessment of the ordination efficiency revealed that the first axis explains 50% of the variation (gradient length 3.3 SD), while the second axis accounts for an additional 23% (gradient length 2.4 SD). The third axis (not shown) accounts for a further 9%, differentiating the Y plots from the R plots, especially in the early stages.

The graph (Fig. 4) shows the development of the restoration plots by their trajectories as well as the reference plots. The reference sites S and T exhibit no successional tendencies and are clearly separated from each other. The trajectories of the restoration plots indicate a notable shift toward the midpoints between the two reference sites, with a clear tendency toward the site that provided the inoculation material (R1–R3: T; R4–R6: S).

An examination of the data from the last 10 years reveals three findings. First, the dynamics of development of the restoration plots have decelerated markedly in recent years. Secondly, the restoration plots R4–R6 have approached the reference site T and moved away from the reference site S. Thirdly, however, the individuality of both restoration plot groups, based on the specific inoculation, has not been completely equalized after 19 years.

The mean Sørensen distances between the restoration plots R1–R3 and their reference site T decreased from 0.83 ± 0.05 in 2005 to 0.47 ± 0.01 in 2023 (p = 0.03, paired sample t-test). This value is identical to that observed in 2014. These values are considerably lower than the mean distances in the reference site S. With regard to plots R4–R6 in comparison with S, the mean Sørensen distances decreased from 0.85 ± 0.01 to 0.50 ± 0.01 in 2014 (p = 0.0001). Since that time, however, there has been a slightly renewed increase to 0.54 ± 0.00 in 2023 (p = 0.02). Over the course of this period, the mean distance to reference site T decreased from 0.57 ± 0.01 to 0.53 ± 0.2 (p > 0.05, not significant). These values are in alignment with the observations previously mentioned.

The younger restoration plots Y1–Y3 exhibited a generally similar development, although it was relatively faster. According to the mean Sørensen distances, these plots were also quite dissimilar to the reference sites S and T at the beginning of 2009: 0.83 ± 0.05 or 0.80 ± 0.04, respectively. By 2023, the values dropped to 0.60 ± 0.04 (p = 0.009) or 0.49 ± 0.02 (p = 0.005), respectively.

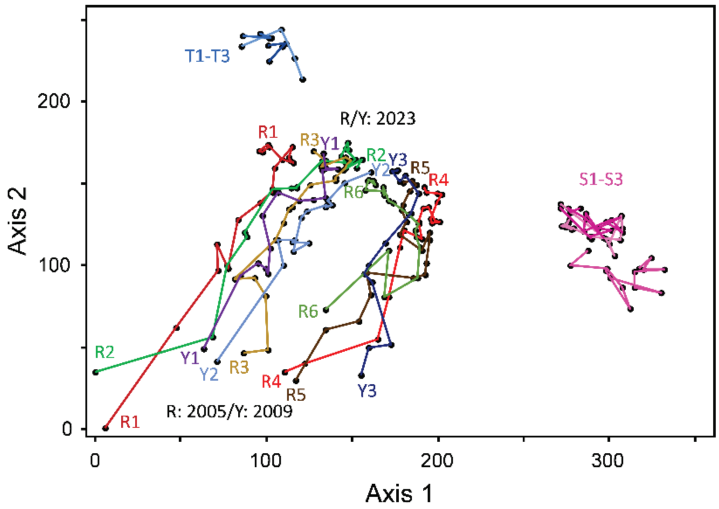


Fig. 4. Detrended correspondence analysis (DCA) of the relevés (including bryophytes and lichens) of the small plots. The Braun-Blanquet data were previously rank-transformed. The time points of each permanent plot were connected by trajectories and distinguished by colors. The trajectories of the restoration plots start at the lower left corner of the graph in 2005 (R plots) or 2009 (Y plots). Axis scaling: 100 = 1 unit of standard deviation (SD). Axis 1 explains 50% and axis 2 another 23% of the variance in the data set.

Abb. 4. Detrended Correspondence Analysis (DCA) der Vegetationsaufnahmen (einschließlich der Moose und Flechten) der kleinen Plots. Die Braun-Blanquet-Daten wurden zuvor rangtransformiert. Die Zeitpunkte jeweils einer Dauerfläche wurden durch Trajektorien verbunden und durch Farben differenziert. Die Trajektorien der Restitutionsfläche beginnen links unten im Diagramm im Jahr 2005 (R-plots) bzw. 2009 (Y-plots). Achsenskalierung: 100 = 1 Standardabweichung (SD). Achse 1 erklärt 50 % und Achse 2 weitere 23 % der Varianz des Datensatzes.

The ordination of the data set with the 79 m² plots (Supplement E1) yielded a nearly identical outcome, but the trajectories exhibit a slightly more condensed bundle structure (see Section 4.1: different plot sizes).

The cluster analysis identified six groups. The assignment of individual points to these clusters is visually represented by colors in Figure 5. The clusters were separated in the following order: (1) reference site S, (2) early stages of the R and Y plots, (3) late stages of R4–R6 and Y3, (4) late stages of Y1–Y2, (5) late stages of R1–R3, and (6) donor site T. Remarkably, the donor sites S and T were not combined into one cluster. In contrast, the late stages of R1–R3 exhibit the highest degree of similarity to donor site T, as shown by the Sørensen distances (see above). All early stages of the restoration plots were grouped together into one cluster, regardless of the origin of the inoculation material and the year when restoration was initiated. The distinction between Y1–Y2 and Y3 has already been addressed.

The relationship between several structural and diversity variables and the position of the plots is also illustrated in Figure 5. The initial restoration stages are distinguished by a high cover of open soil and a high number of *Stellarietea* species. The reference site T displays the highest number and cover of *Koelerio-Corynephoretea* species and the largest TSR_{quant}. In contrast, the reference site S exhibits the highest number of *Festuco-Brometea* species,

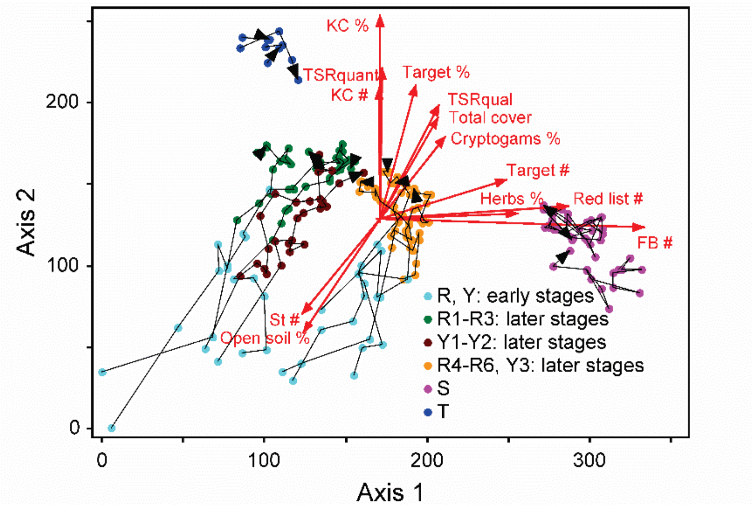


Fig. 5. Detrended correspondence analysis (DCA) as in Figure 4, but with the colors of the plots indicating their assignment to six clusters as determined by cluster analysis. The vectors representing the structural and diversity variables are presented in red. Only variables with a coefficient of determination (r^2) exceeding 0.3 with the ordination axes were included. # = number of species, % = sum of cover percentages, FB = *Festuco-Brometea*, KC = *Koelerio-Corynephoretea*, St = *Stellarietea mediae*, Target = target species, Red list # = number of red-listed/near-threatened species.

Abb. 5. Detrended correspondence analysis (DCA) wie in Abbildung 4, aber die Farben der Plots geben die Zuordnung zu den sechs Clustern an, die durch die Clusteranalyse ermittelt wurden. Die Vektoren der Struktur- und Diversitätsvariablen sind rot eingetragen. Nur Variablen mit einem Bestimmtheitsmaß (r^2) von über 0,3 mit den Ordinationsachsen wurden berücksichtigt. # = Artenzahl, % = Deckungssumme, FB = *Festuco-Brometea*, KC = *Koelerio-Corynephoretea*, St = *Stellarietea mediae*, Target = Zielarten, Red list # = Zahl der Rote Liste-Arten einschließlich Arten der Vorwarnliste.

red-listed/near-threatened species, and target species, as well as the highest cover of herbs. Both donor sites are characterized by a high cover of target species, bryophytes/lichens, and total vegetation, as well as a high TSR_{qual}.

The DCA diagram, which depicts the estimated species optima (Supplement E2), provides further insights into these statements. The lower portion of the figure, which represents the initial years following the commencement of restoration, is dominated by *Stellarietea* species. In the center of the diagram, *Koelerio-Corynephoretea* and *Festuco-Brometea* species are concentrated, which were observed in the reference and restoration plots. Some of the later successional species that were not successfully transferred to the restoration site (see Section 3.2) are displayed in the area of donor site S, and the same is true for some pioneer species near donor site T.

3.4 Structural and diversity variables

3.4.1 Species numbers and sum of cover percentages

The mean numbers of all species, including bryophytes/lichens, per plot for the 79 and 25 m² plots are presented in Figure 6. At the 79 m² R plots (solid lines), the number of species initially increased from 24 ± 2 in the 1st year to a peak of 40 ± 1 in the 5th year

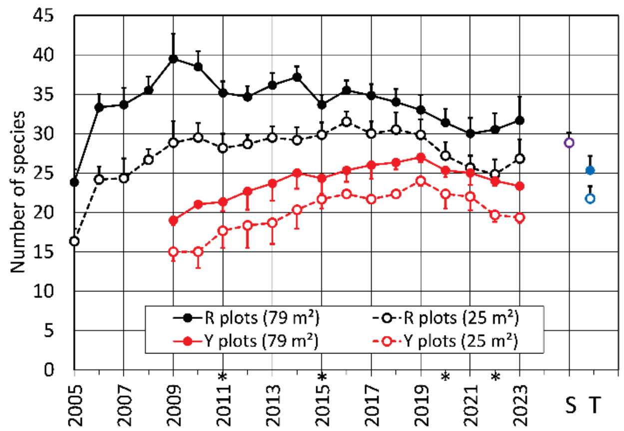


Fig. 6. Mean number of species of the restoration plots (black: R, red: Y) over the course of the study period. The plots at the reference sites are depicted in purple (S) or blue (T) on the right side of the diagram. Solid lines and filled symbols: large plots, dashed lines and open symbols: small plots. Error bars indicate the standard errors of the six (R) or three plots (Y, S, T). Asterisks (*) on the time axis denote years with extreme heat and/or drought periods.

Abb. 6. Mittlere Artenzahlen der Restitutionsflächen (schwarz: R, rot: Y) im Verlauf der Untersuchungsperiode. Die Plots der Referenzflächen sind in violett (S) bzw. blau (T) rechts im Diagramm eingetragen. Durchgezogene Linien und ausgefüllte Symbole: große Plots, gestrichelte Linien und offene Symbole: kleine Plots. Die Fehlerbalken geben die Standardfehler der sechs (R) bzw. drei Plots (Y, S, T) an. Die Sterne (*) an der Zeitachse kennzeichnen die Jahre mit extremer Trockenheit und/oder Hitze.

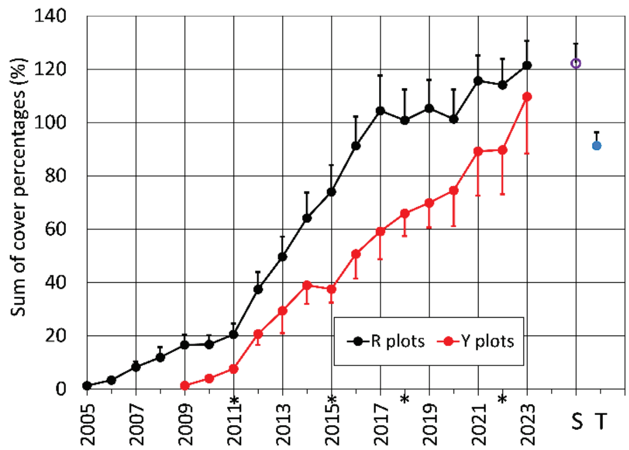


Fig. 7. Mean sum of cover percentages for all species of the large restoration plots (black: R, red: Y) over the course of the study period. The plots at the reference sites are depicted in purple (S: small plots) or blue (T) on the right side of the diagram. Error bars indicate the standard errors of the six (R) or three plots (Y, S, T). Asterisks (*) on the time axis denote years with extreme heat and/or drought periods.

Abb. 7. Mittlere Deckungssummen aller Arten der großen Restitutions-Plots (schwarz: R, rot: Y) im Verlauf der Untersuchungsperiode. Die Plots der Referenzflächen sind in violett (S: kleine Plots) bzw. blau (T) rechts im Diagramm eingetragen. Die Fehlerbalken geben die Standardfehler der sechs (R) bzw. drei Plots (Y, S, T) an. Die Sterne (*) an der Zeitachse kennzeichnen die Jahre mit extremer Trockenheit und/oder Hitze.

following the commencement of restoration. Over the past 9 years, the number of species fluctuated between 30 ± 2 and 36 ± 1. In contrast, the species numbers on the large Y plots were lower, with a peak of 27 ± 1 occurring only in the 11th year after restoration commencement. A subsequent slight decline to 23 ± 0.3 was observed in 2023.

The same general tendencies were observed at the 25 m² plots (dashed lines in Fig. 6), but with consistently lower species numbers. The number of species in the smaller plots was found to be 69–77% of that in the 79 m² plots in the first 6 years at the R plots and 71–79% in the first 2 years at the Y plots. Following this initial period, the values increased to 80–90% at all plots. The lower values observed at the outset are likely attributable to a high proportion of species with scattered occurrence. As vegetation cover increased, smaller plots were more likely to capture the majority of species present. Due to the superior representation of species at the larger plots, the subsequent analysis will focus on the results of the 79 m² plots (with the exception of the reference site S, where only small plots were surveyed). The phytodiversity observed in the restoration plots over the past 10 years is comparable to that observed at the reference sites S (29 ± 1 at the smaller plots) and T (25 ± 2 at the larger plots, 22 ± 2 at the smaller plots). With regard to the sum of cover percentages for all species within the plots, the picture is distinctly different (Fig. 7). In the initial year following the commencement of restoration, the cumulative cover percentages of all species together reached only 1% of the ground at the R and Y plots. At the R plots, the increase in cover percentage was slow for 6 years, followed by a more rapid increase for 6 years, reaching a cover percentage exceeding 100% by the 13th year. Due to the overlapping of plants, this value continued to increase during the following years, although at a slower rate. A comparable yet more uniform increase in cover can be observed at the Y plots (red line in Fig. 7). The maximum values were reached at the R plots (121 ± 9%) and Y plots (110 ± 21%) in the final years. It was only at this point that the sum of cover percentages at the reference site S (122 ± 7%) was reached or nearly reached. At the reference site T, with a vegetation that exhibited more pronounced pioneer characteristics, the value was lower (91 ± 5%).

3.4.2 Life form spectra

The spectra of the proportions of life forms in the number of species at the restoration and reference plots (Fig. 8) reveal a high diversity. The most prevalent groups in terms of species numbers were annuals and hemicryptophytes. Both occurred nearly equally at the restoration plots, while annuals dominated reference site T and hemicryptophytes reference site S. Another striking fact is the relatively high stability during the development of the restoration plots. The most notable change was a decrease in the contribution of annuals over the first 4 years.

The proportions of life forms to the vegetation cover were found to be disparate (Fig. 9). Following the commencement of restoration, annuals were the dominant life form for the first 2 years. However, they subsequently declined largely, with the exception of the final year, during which *Bromus tectorum* exhibited a higher abundance at the restoration plots (see Section 4.1). Geophytes (and to a lesser extent also juvenile phanerophytes) played a transient role after the decrease in annuals for a few years (R plots) or many years (Y plots). Thereafter, the cover of phanerogams was predominantly formed by hemicryptophytes and chamaephytes.

Bryophytes/lichens were of minimal importance during the initial stages of the restoration plots, but their cover increased gradually. At the R plots, the cryptogams exceeded the cover of the phanerogams since the 14th year. Lichens played a negligible role. With regard

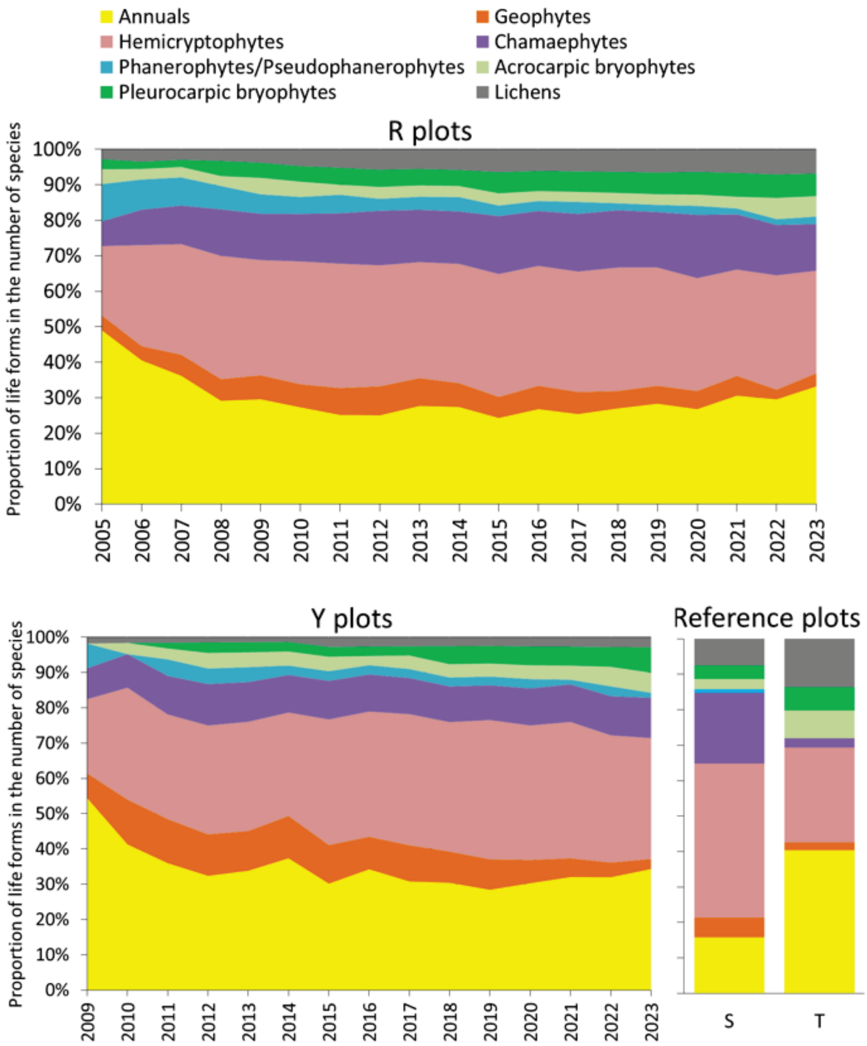


Fig. 8. Spectra of the proportions of the life forms in the number of all species of the large restoration and reference plots over the course of the study period (S: small plots). Means of the six (R) or three plots (Y, S, T) were calculated.

Abb. 8. Spektren der Anteile der Lebensformen an der Gesamtartenzahl der großen Restitutions- und Referenz-Plots im Verlauf der Untersuchungsperiode (S: kleine Plots). Es wurden die Mittelwerte der jeweils sechs (R) bzw. drei Plots (Y, S, T) berechnet.

to bryophytes, acrocarpic species were the most prevalent. Pleurocarpic species exhibited a subordinate presence, particularly at the Y plots.

The reference sites S and T exhibited pronounced differences. The vegetation cover of site T was composed almost exclusively of acrocarpic bryophytes and hemicryptophytes, while site S, with a more balanced life form spectrum, resembled the later stages of the restoration plots. However, lichens were notably prevalent here, with conversely fewer bryophytes.

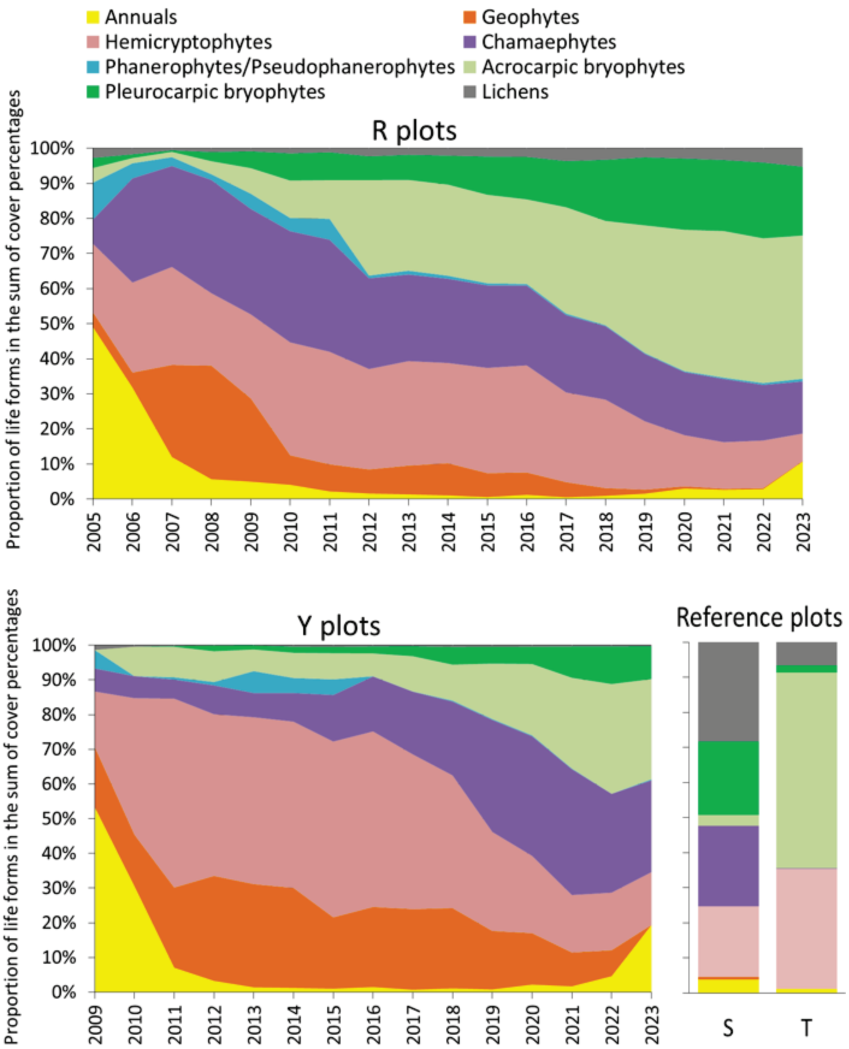


Fig. 9. Spectra of the proportions of the life forms in the sum of cover percentages of all species of the large restoration and reference plots over the course of the study period (S: small plots). Means of the six (R) or three plots (Y, S, T) were calculated.

Abb. 9. Spektren der Anteile der Lebensformen an der Deckungssumme aller Arten der großen Restitutions- und Referenz-Plots im Verlauf der Untersuchungsperiode (S: kleine Plots). Es wurden die Mittelwerte der jeweils sechs (R) bzw. drei Plots (Y, S, T) berechnet.

3.4.3 Phytosociological spectra

To gain further insights into the underlying processes of development, the species were displayed according to their assignment to phytosociological classes.

When the proportions in species numbers are considered (Fig. 10), many *Stellarietea* species occurred in the initial stage of development, and they characterized a *Stellarietea* stage for 3 years, but the proportion was always < 40%. By the 4th year, the proportion of

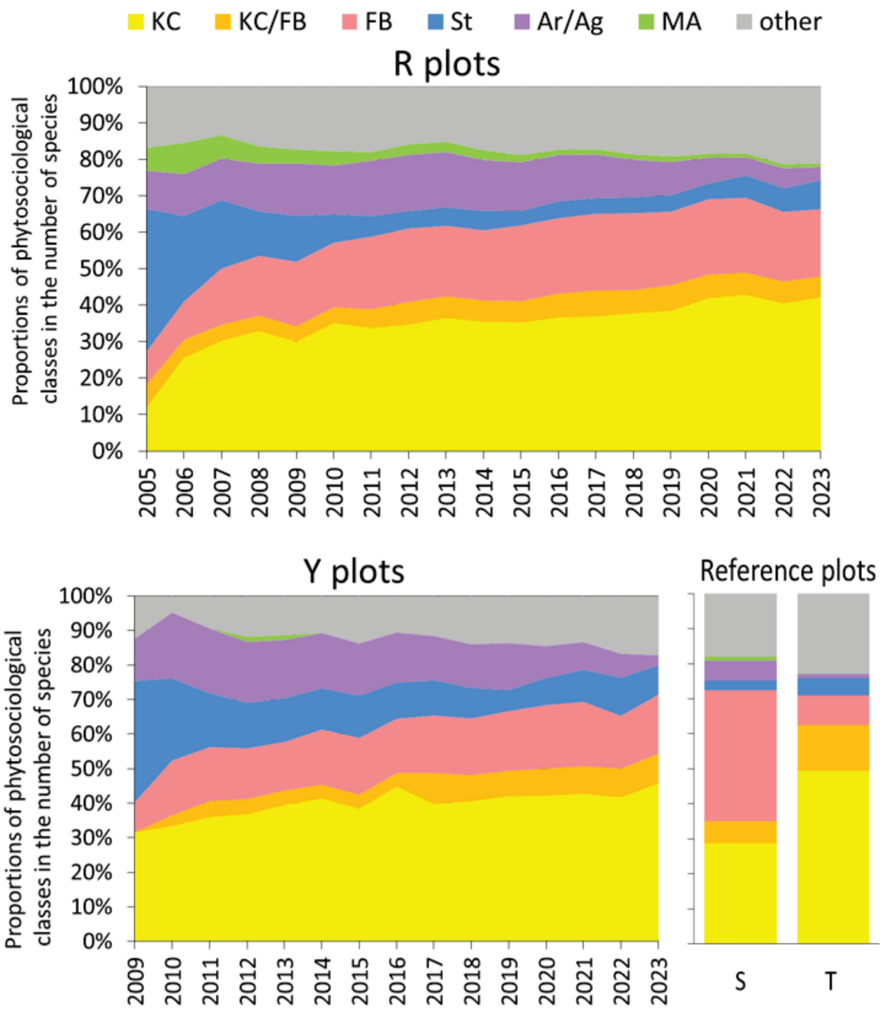


Fig. 10. Spectra of the proportions of the phytosociological classes in the number of all species of the large restoration and reference plots over the course of the study period (S: small plots). Means of the six (R) or three plots (Y, S, T) were calculated. KC = *Koelerio-Corynephoretea*, FB = *Festuco-Brometea*, St = *Stellarietea mediae*, Ar/Ag = *Artemisietea*/*Agropyretea*, MA = *Molinio-Arrhenatheretea*.

Abb. 10. Spektren der Anteile der pflanzensoziologischen Klassen an der Gesamtartenzahl der großen Restitutions- und Referenz-Plots im Verlauf der Untersuchungsperiode (S: kleine Plots). Es wurden die Mittelwerte der jeweils sechs (R) bzw. drei Plots (Y, S, T) berechnet. KC = *Koelerio-Corynephoretea*, FB = *Festuco-Brometea*, St = *Stellarietea mediae*, Ar/Ag = *Artemisietea*/*Agropyretea*, MA = *Molinio-Arrhenatheretea*.

this species group had diminished substantially (12% or 13% at the R or Y plots, respectively). Ruderal species of the *Agropyretea* or *Artemisietea* classes persisted for a longer time (at the Y plots, *Equisetum arvense* and, temporarily, *Calamagrostis epigejos* or *Cynodon dactylon*), but they also became increasingly negligible. The same is true for *Molinio-Arrhenatheretea* species, which in any case were of minor importance. The

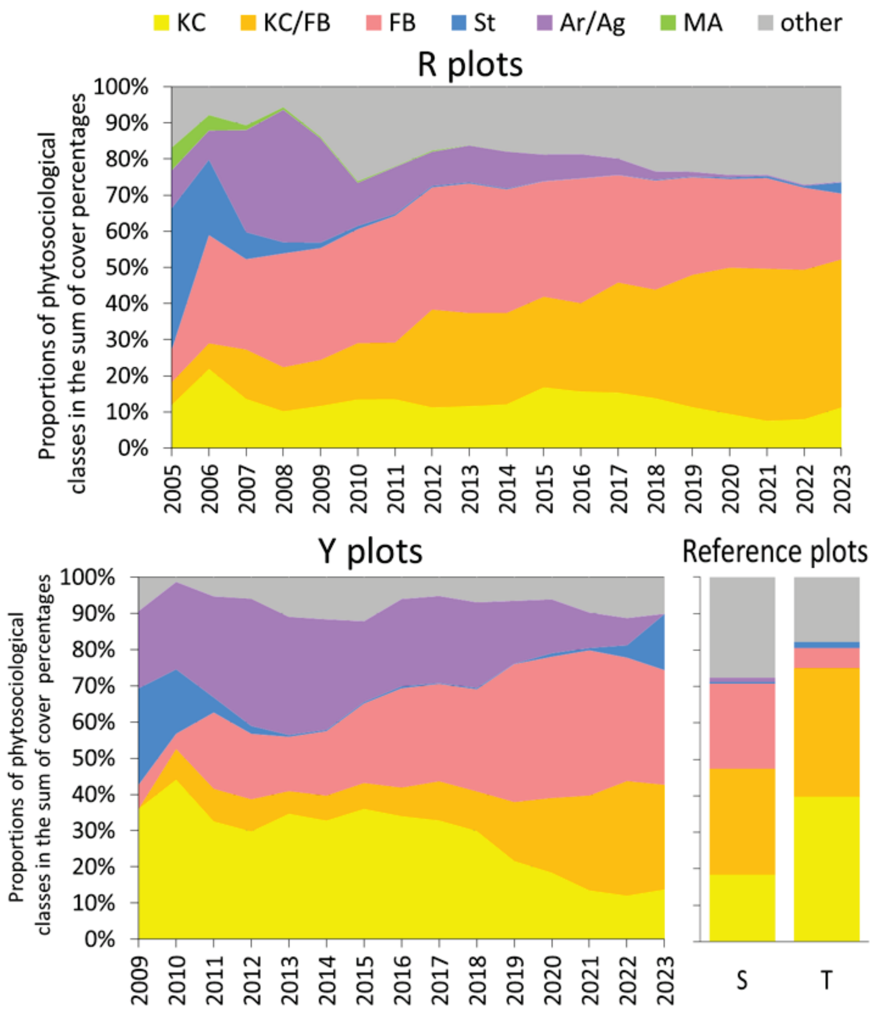


Fig. 11. Spectra of the proportions of the phytosociological classes in the sum of cover percentages of the large restoration and reference plots over the course of the study period (S: small plots). Means of the six (R) or three plots (Y, S, T) were calculated. KC = *Koelerio-Corynephoretea*, FB = *Festuco-Brometea*, St = *Stellarietea mediae*, Ar/Ag = *Artemisietea*/*Agropyretea*, MA = *Molinio-Arrhenatheretea*.

Abb. 11. Spektren der Anteile der pflanzensoziologischen Klassen an der Deckungssumme aller Arten der großen Restitutions- und Referenz-Plots im Verlauf der Untersuchungsperiode (S: kleine Plots). Es wurden die Mittelwerte von jeweils sechs (R) bzw. drei Plots (Y, S, T) berechnet. KC = *Koelerio-Corynephoretea,* FB = *Festuco-Brometea,* St = *Stellarietea mediae,* Ar/Ag = *Artemisietea/Agropyretea,* MA = *Molinio-Arrhenatheretea.*

proportion of *Koelerio-Corynephoretea* species initially accounted for 12% (R plots) or 31% (Y plots) of the species, and their importance steadily increased. This trend was also observed for *Festuco-Brometea* and overarching species. Overall, it should be noted that, over the time course, the relative contribution of species groups was very similar between R and Y plots.

A high degree of similarity in species composition is also evident when comparing the later stages of the restoration sites with the reference sites. In particular, the proportion of later-successional *Festuco-Brometea* species is particularly high at reference site S, while it is relatively low at reference site T. The opposite is true for the proportion of species assigned to the *Koelerio-Corynephoretea* class. At site T, there were 11 ± 1 *Koelerio-Corynephoretea* species but only 2 ± 0 *Festuco-Brometea* species, whereas at site S there were 8 ± 1 and 11 ± 3 species, respectively. In this respect, the restoration plots were much more similar to site T. The number of species of the *Koelerio-Corynephoretea* class was 12–14 (R plots) or 9–11 (Y plots), and that of the *Festuco-Brometea* class was only 6–7 (R plots) or 4–5 (Y plots). These numbers were stable within the indicated range since the 4th (R plots) or 5th (Y plots) year. The relative proportions, particularly of *Koelerio-Corynephoretea* species, exhibited an even increase due to declines in other species groups (Fig. 10).

With regard to the proportions of the phytosociological classes in the vegetation cover (Fig. 11), it is evident that similar but much more pronounced displacements have occurred. The contribution of *Stellarietea* species exhibited a steep decline, reaching negligible levels (< 5%) by the 3rd year (with the exception of *Bromus tectorum* in the final year, as previously noted). Ruderal species of the *Agropyretea* or *Artemisietea* classes were able to build up substantial cover in the following stage, but they were subsequently eliminated, either rapidly (R plots) or more slowly (Y plots), to minimal values. The proportion of *Koelerio-Corynephoretea* species reached a peak in the 2nd year and remained relatively stable in the following years (R plots) or exhibited a decline (Y plots). At the R and Y plots, the *Festuco-Brometea* and overarching species demonstrated a marked expansion in the later years. While a slight reduction in *Festuco-Brometea* species was observed at the R plots over the past decade, the Y plots demonstrated a continued dominance of *Festuco-Brometea* species. This can be attributed to a single species, *Artemisia campestris*, with a mean cover of 13–32% over the last 6 years.

A comparison of the restoration plots with the reference sites over recent years reveals a high degree of similarity, particularly with site S.

3.4.4 Measures of restoration success

In the initial year, the TSR_{qual} value (solid lines in Fig. 12) was found to be relatively low at the R plots (0.27 ± 0.02), in contrast to the Y plots, where it was observed to be higher (0.40 ± 0.04). In the following years, there was a marked increase, which subsequently levelled off and peaked in 2021 for the R plots (0.70 ± 0.01) and in 2023 for the Y plots (0.71 ± 0.02). It took these extended periods to reach the benchmark of the reference sites S (0.72 ± 0.04) and T (0.69 ± 0.01). The increase in TSR_{qual} was a consistent trend over a period of 15 (Y plots) or 17 (R plots) years. In the initial and intermediate stages, the primary driver was a more pronounced expansion in the number of target species relative to all species (Supplement E3). In the later stages, the primary cause was a reduction in the total number of species, while the number of target species remained relatively stable. Since the 5th year, the absolute number of target species was in the range of 20–23 (R plots) or 14–18 (Y plots), which is similar to the number of target species in our reference plots of 21 ± 1 (S plots) or 17 ± 1 (T plots).

TSR_{quant} commenced (dashed lines in Fig. 12) with the same initial values as TSR_{qual}, due to the equal smallest possible cover estimates for all species. However, in the following years, TSR_{quant} was consistently higher, indicating that target species were more able to attain higher cover than non-target species. After the 8th (R plots) or 11th year (Y plots), a plateau

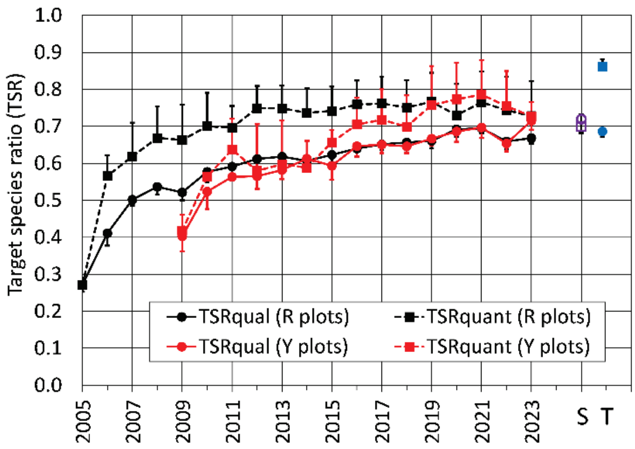


Fig. 12. Mean target species ratios (TSR) of the large restoration plots (black: R, red: Y) over the course of the study period. The plots at the reference sites are depicted in purple (S) or blue (T) on the right side of the diagram (S: small plots). Solid lines and round symbols: TSR_{qual}, dashed lines and quadrats: TSR_{quant}. Error bars indicate the standard errors of the six (R) or three plots (Y, S, T).

Abb. 12. Mittlere Zielarten-Ratios (TSR) der großen Restitutions-Plots (schwarz: R, rot: Y) im Verlauf der Untersuchungsperiode. Die Plots der Referenzflächen sind in violett (S) bzw. blau (T) rechts im Diagramm eingetragen (S: kleine Plots). Durchgezogene Linien und runde Symbole: TSR_{qual}, gestrichelte Linien und quadratische Symbole: TSR_{quant}. Die Fehlerbalken geben die Standardfehler der sechs (R) bzw. drei Plots (Y, S, T) an.

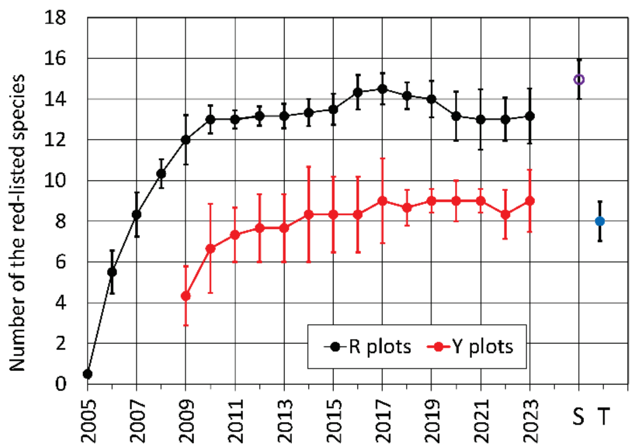


Fig. 13. Mean number of the red-listed (including near-threatened) species of the large restoration plots (black: R, red: Y) over the course of the study period. The plots at the reference sites are depicted in purple (S: small plots) or blue (T) on the right side of the diagram. Error bars indicate the standard errors of the six (R) or three plots (Y, S, T).

Abb. 13. Mittlere Anzahl der Rote Liste-Arten (einschließlich Arten der Vorwarnliste) der großen Restitutions-Plots (schwarz: R, rot: Y) im Verlauf der Untersuchungsperiode. Die Plots der Referenzflächen sind in violett (S: kleine Plots) bzw. blau (T) rechts im Diagramm eingetragen. Die Fehlerbalken geben die Standardfehler der sechs (R) bzw. drei Plots (Y, S, T) an.

was reached where TSR_{quant} stabilized. The maximum values were 0.77 ± 0.08 (R plots) or 0.79 ± 0.09 (Y plots). These values are within the benchmark values set by the reference sites: 0.70 ± 0.03 (S) or 0.86 ± 0.02 (T). The exceptionally high value observed at site T is attributed to the high cover percentages of *Syntrichia ruralis* var. *ruraliformis* (mean: 46%). A comparison of the TSR values of the 79 m² plots and the 25 m² plots is illustrated in Supplement E4. The curves exhibit a high degree of similarity for both plot sizes.

Apart from the creation of habitats for target species, restoration efforts are also directed toward red-listed species. The numbers of these endangered species at the R plots exhibit a marked increase from 0.5 ± 0.2 species in the 1st year to at least 13.0 species from the 6th year onward (Fig. 13). In 2017, a maximum of 14.5 ± 0.8 species was reached. In the last 3 years (after 16 years), there was a tendency toward a decline at the R plots. Species such as *Veronica verna*, *Orobanche arenaria*, and *Koeleria macrantha* were no longer present (see Supplement S1), but *Orobanche arenaria* still occurred outside the plots in 2024. At the Y plots, 4.3 ± 1.2 endangered species were found in the 1st year, and a plateau of 8.3–9.0 species was reached after the 6th year. The values fell within the range of red-listed/near-threatened species numbers at reference sites T (8.0 ± 1.0) and S (15.0 ± 1.0).

3.5 Impact of heat and drought years

As previously stated in Section 2.1, 4 years of the investigation period were identified as being characterized by exceptional heat and/or drought spells: 2011, 2015, 2018, and 2022 (see Fig. 14 for details of heat waves and strong drought periods). The consequences of such extreme weather conditions can be observed in Fig. 6. The number of species declined in 2011 (R), 2015 (R and Y), and 2022 (Y), or the increases were below expectations (2011: Y). Additionally, the sum of cover percentages (Fig. 7) demonstrated declines (2015: Y; 2018: R; 2022: R) or fell below expectations (2011: R and Y; 2022: Y).

Previous studies in our area have shown a pronounced impact, particularly on the species number of annuals (see Section 1). As can be gathered from Fig. 14, the impact at the restoration site of the current study (R and Y plots) was less pronounced than that at the target areas studied in previous publications (see Section 1): the “Griesheimer Düne” (GD, three plots) and the “Ehemaliger August-Euler-Flugplatz” (AEF, seven plots). In order to ensure optimal comparability, the data of the 25 m² plots were used for this diagram, which was also the plot size at the target areas named above. All plots were managed by grazing.

4. Discussion

4.1 Was there a continuous development of red-listed/near-threatened plant species and target species in general?

For most of our analyses (especially concerning rarer species), it was useful to apply the **two different plot sizes**. With the smaller plots, we had a suitable size for the comparison with the plots of target site S, which have the same size. With the larger plots, we were able to record rarer or accidental species more appropriately (this is also reflected in the more condensed bundle structure of the trajectories in the DCA graph based on the larger plots). In smaller plots, stochastic floristic variation may lead to more between-plot floristic differences than in larger plots (Otýpková & Chytrý 2006).

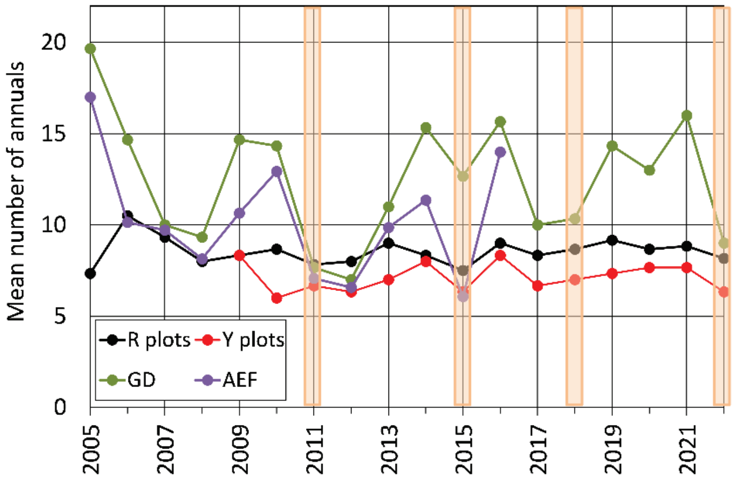


Fig. 14. Mean numbers of annuals at the restoration plots (R, six plots, Y, three plots) over the course of the study period compared to two target areas: "Griesheimer Düne" (GD, three plots) and "Ehemaliger August-Euler-Flugplatz" (AEF, seven plots). Beige bars: years with extreme heat and/or drought periods. Data for extreme heat/drought years for Frankfurt International Airport (www.wetter-kontor.de); in brackets: differences from average 1961–1990. 2011 heavy dry periods in spring (-59.3% precipitation); 2015 heavy dry periods in spring (-60.7% precipitation); 2018 heavy heat waves in summer (+2.2 °C) and heavy dry periods in summer (-68.3% precipitation); 2022 heavy heat waves in summer (+2.4 °C) and heavy dry periods in summer (-59.4% precipitation).

Abb. 14. Mittlere Zahl der Therophyten der Restitutions-Plots (R, sechs Plots, Y, drei Plots) im Verlauf der Untersuchungsperiode verglichen mit zwei Leitbildflächen: „Griesheimer Düne" (GD, drei Plots) und „Ehemaliger August-Euler-Flugplatz" (AEF, sieben Plots). Beige Balken: Jahre mit extremen Hitze- und/oder Dürreperioden. Daten für extreme Jahre mit Hitze/Trockenheit für Frankfurt International Airport (www.wetterkontor.de); in Klammern: Abweichungen vom Mittelwert 1961–1990. 2011 starke Trockenperioden im Frühling (-59,3 % Niederschlag); 2015 starke Trockenperioden im Frühling (-60,7 % Niederschlag); 2018 heftige Hitzewellen im Sommer (+2,2 °C) und starke Trockenperioden im Sommer (-68,3 % Niederschlag); 2022 heftige Hitzewellen im Sommer (+2,4 °C).

The sums of red-listed/near-threatened species were high (> 13 at the R plots and > 8 at the Y plots) since the 6th year, but they decreased slightly in the last 3 years at the R plots. For example, both *Fumana procumbens* and *Dianthus carthusianorum* vanished on one plot, and the near-threatened species *Helianthemum nummularium* subsp. *obscurum* on four plots. The number of red-listed/near-threatened species of the reference area S (15) was not achieved, but on this site there are more *Festuco-Brometea* species that are elements of a later stage of development (e.g., *Scabiosa canescens*).

The development of selected very rare red-listed species will be discussed in the following:

– ***Alyssum gmelinii***

The species (red-listed, category 2) has been revised taxonomically, with the result that there is a geographical separation between *Alyssum montanum* and *A. gmelinii* (Thiv et al. 2022). In the following, we focus on the occurrences of *A. gmelinii* on sandy substrate. The plant species strongly decreased in the sandy areas of Hesse (Hodvina & Cezanne 2007b). Some approaches have been taken in our area to enlarge the population sizes by restoration measurements: (1) in the study site “corridor” Seeheim-Jugenheim and (2) in the “Griesheimer Sand” west of Darmstadt on three “neodunes“ in the frame of our epizoochory experiment (see above and Wessels-de Wit & Schwabe 2010). In the corridor, the species showed an establishment already in the 2nd year (R plots) and in the 1st year (Y plots), and it colonized all plots until the 4th/5th year. The plant species showed excellent vitality with high seed production. Hodvina & Cezanne (2007b) counted about 150 plants in 2006 (the 2nd and 1st years of appearance). After 20 years (2024), we counted 1230 (R plots) and 300 (Y plots) plants. Many species of the *Brassicaceae* are not self-compatible, so cross-pollination is essential. Krausch (2011) detected a rich wild-bee fauna on the corridor, with *A. gmelinii* as a key resource for pollen and nectar. Ten *Andrena* species (including the endangered *Andrena argentata*) were verified between 2007 and 2024 (Krausch & Kratochwil n. p.). In the litter layer of reference site S, we found seeds that germinated successfully (Krolupper & Schwabe 1998), showing that seeds of *A. gmelinii* are also transferred by raking techniques. In 2006, the reference site S had a very high number of specimens (about 10,000 according to Hodvina & Cezanne 2007b). In the “neodune” site of the “Griesheimer Sand”, *A. gmelinii* was dispersed by seeds that were experimentally attached to sheep fur (a model for our connectivity approach with sheep dispersal). The successful development has been monitored for 10 years until now (Storm et al. 2022). Dispersal to the marginal zone of the site was observed up to 12 m away (but restricted to the deposited deep-sand area: Weißmantel in Storm et al. 2022).

– ***Fumana procumbens***

This rare species (red-listed, category 2) has a very scattered distribution in Germany, growing in the driest wing of *Festuco-Brometea* communities and in *Koelerion glaucae* sites. The long-lived perennial dwarf shrub shows no clonal growth (Dahlgren et al. 2016), so all plants on our restoration site come from seedlings. *F. procumbens* has high vitality in the corridor, with a high production of seeds. The species was visited by *Andrena barbilabris*, a target wild-bee species for sandy habitats (Krausch & Kratochwil n. p.). In the reference site S, we found the species in the litter layer and verified successful germination (Krolupper & Schwabe 1998). In the reference site S (0.7 ha), Hodvina & Cezanne (2007a) counted 1,169 specimens in 2006, which was the largest population in southern Hesse. Already in the 2nd year, the plant species established itself on two R plots and later on three to four R plots and one Y plot. Hodvina & Cezanne (2007a) counted 43 specimens in 2006. In the 5th year, four R plots had been colonized, probably from seeds in the raked material and not by transfer from the donor site; only one Y plot had been colonized. In 2024, we found about 50 specimens on the old corridor (R) and about 100 on the new parts (Y).

– ***Jurinea cyanoides***

Jurinea cyanoides occurs in the upper northern Rhine valley on the western edge of the distribution area. In the corridor experiment, we were able to establish a population of this rare species (red-listed, category 2, FFH appendix II) only for a short time period. Considering that we did not find the species in the seed bank (Krolupper & Schwabe 1998) and that fruit predation is high (Eichbeg et al. 2005), even that is remarkable. The small population on the corridor had only about 40 rosettes in 2010. In the Y plots, the plant species occurred from 2010 to 2014; in 2020, there were 39 rosettes left outside the plots, and they vanished totally in 2022 (HLNUG 2022). The tiny population of the S reference area showed a decline from about 400 rosettes during the time of the construction of the

Y plots to only about 80 rosettes in 2022 (HLNUG 2022). The reasons for this decrease could not be detected (stochastic processes in a small population?), as in various other sites, also according to the newest monitoring (HLNUG 2022). A tiny population additionally introduced in 2020 on the southern corridor outside the plots (HLNUG 2022) was not part of our experiment. In an area belonging to the "Griesheimer Sand" west of Darmstadt, where we constructed three "neodunes" with deep sand and carried out a sheep-epizoochory experiment with *J. cyanoides* and other *Koelerion glaucae* species, a *J. cyanoides* population had established itself since 2010 (Storm et al. 2022). The ecological conditions are very similar to those of the corridor, and the site was also grazed by donkeys.

Very successful restoration approaches for the establishment and development of *J. cyanoides* populations were taken in Saxony-Anhalt. This area represents, also from a biogeographical point of view, more subcontinental conditions than the Upper Rhine valley. The proposal of Tischew et al. (2017) is a "drastic site-preparation for the re-introduction of *Jurinea*". According to the authors, the removal of the topsoil is often necessary to establish nutrient-poor conditions and low competition (in the two cases reported above, this is solved by the deposition of deep sand). The compilation of the local authorities for nature protection (including different restoration projects of the group of Sabine Tischew, as well as restored sites in Saxony-Anhalt) shows mostly good developments for this plant species. Horse grazing was a management measure (with effects comparable to our donkey grazing), and one of these sites showed an increase from 1,600 to 15,000 rosettes in 8 years (Krumbiegel et al. 2022).

In Hesse, there are only about 30 mostly small sites with *J. cyanoides* populations left (about one-half with newly established populations after 2003). Only one-third of these sites showed a tendency of increasing numbers of rosettes (HLNUG 2022). Our restoration site in the "Griesheimer Sand" (see above) shows a certain stability, with about 400 to 500 rosettes in the last 5 years (HLNUG 2022).

– ***Poa badensis***

This rare species (red-listed, category 2) lives in the study area at the northwestern edge of the distribution area; some more western occurrences are found only in Rhineland-Palatinate (west side of the Rhine valley). The populations of this area mostly have low genetic diversity, but no reduced reproductive success. Therefore, there is evidence of long-term separation, which substantiates the hypothesis that it is a relict species of a former postglacially steppe complex, so it has great value from the viewpoint of biogeography and nature conservation (Plenk et al. 2019).

There is hardly any seed bank of *Poa badensis*. We found only one viable seed in the seedbank of sand ecosystems of the Darmstadt area, but 17 viable seeds in the litter layer of reference site S (Krolupper & Schwabe 1998). Therefore, our method of inoculation, using raking techniques, should lead to successful transfers of this plant species, which was shown not only for the experiment described here but also for two further restoration sites (Stroh 2006).

Already in the 2nd year (R plots) or at once (Y plots), the species established itself on some of the R and Y plots for the entire time window. The reference and donor area S in the direct vicinity of the corridor had a population of about 500 specimens of *Poa badensis* in 1998 and 2007 (Hodvina & Cezanne 2008).

4.2 Was there a successful establishment and development of the endangered pioneer stages of subcontinental calcareous sand vegetation (*Koelerion glaucae*) as well as to a lesser extent more consolidated stages and how can the development be described over the extended period of 19 years?

We already reported about the successful **establishment and development of *Koelerion glaucae* vegetation** in the first 4 and 10 years (Eichberg et al. 2010, Storm et al. 2016). Moreover, our data show that this vegetation type is still intact on the older restoration site R after 19 years and on the younger Y site after 15 years. The Y site is relatively extreme, with inclinations of about 15° and the partial erosion of the loose sand, which causes sand dynamics additionally to the impact of donkeys. The typical *Koelerion glaucae* species *Alyssum gmelinii* (all R and Y plots) and *Poa badensis* (parts of the R and Y plots) are still present (see Section 4.1 for details). According to our results, the phytosociological spectrum of the species composition reveals an increase in the relative importance of *Koelerio-Corynephoretea* species and a relative stability in absolute numbers.

On an older restoration site in the direct vicinity, Stroh (2006) observed the grazing preferences of donkeys and recorded that *A. gmelinii*, *K. glauca*, and *P. badensis* were not grazed. Our investigations in similar vegetation types in the wider area have shown that donkey grazing has the following remarkable effects: the successful reduction in ruderal perennial herbs/graminoids and the creation of open sites by wallowing in the sand; therefore, they are "processors of a special vegetation pattern" (Süß & Schwabe 2007). Similar results have been found in, for example, coastal sand dunes in Belgium (Lamoot et al. 2005). As a rule, the dominance structures of plant species are often reduced by grazing, as a worldwide meta-study by Koerner et al. (2018) has shown.

Further developments in the direction of ***Allio-Stipetum* vegetation** (*Festuco-Brometea*), which would be the next step in succession, as we have shown by longtime permanent-plot studies in the wider area (Süß et al. 2010), are scarce until now. By placing the plots of reference site S in a separate cluster, the cluster analysis underlines the relatively large distance of the plots of reference site S from all other plots. The main "species gap" can be found in the *Festuco-Brometea* species of donor site S, especially *Scabiosa canescens*, *Centaurea scabiosa*, *Bromus erectus*, *Medicago falcata*. The ordination graph and the Sørensen distances even showed that the restoration plots R4–R6 moved away in the later years from the reference site S which represents a higher proportion of *Festuco-Brometea* species. The phytosociological spectra demonstrate also a relatively stable proportion of the *Festuco-Brometea* class in relation to species numbers and a decreasing contribution to vegetation cover at the R plots. The higher importance at the Y plots over the past 6 years was attributed to a single species, *Artemisia campestris*. *Stipa capillata* established itself for some years in a few plots (R and Y), but it did not resist the grazing pressure of the donkeys. At once or after some years, other *Festuco-Brometea* species, such as *Asperula cynanchica* and *Helianthemum nummularium* subsp. *obscurum*, were successful in establishing themselves for the whole time in the R plots and partly in the Y plots. The frequent species *Euphorbia seguieriana* and *Fumana procumbens* are supraregionally assigned to *Festuco-Brometea* communities (Oberdorfer 2001), but they characterize also more developed *Koelerion glaucae* vegetation in the Northern Rhine valley (Korneck 1974, Oberdorfer 2001). Therefore, they should not be regarded as strong indicators of further development. This development will take more time since the soil on the corridor site is still mainly undeveloped. The same result of such "species gaps" on undeveloped soil was shown by Hofmann et al. (2020) in a study in Bavaria near the "Garchinger Heide" with the aim to restore calcareous grassland. For our concept to restore mainly *Koelerion glaucae* vegetation it is a remarkable result that from the *Koelerion glaucae/Allio-Stipetum* vegetation complex of site S this "species gap" can only be stated for some *Allio-Stipetum* (*Festuco-Brometea*) species, which is in line with the aim of our restoration project.

The **inoculation source (donor site) modulated the floristic structure of the R plots**, with some differentiating species from the beginning of the experiment until the tentative end, which is shown in the ordination diagram and by the Sørensen distances. This indicates that the initial inoculation has not been obliterated by dispersal processes, even over a long period of time and a short distance. This is compatible with the classical concept of Egler (1954) about the "initial floristic composition". Dispersal processes of new target species from the vicinity could not be recorded, although there were (albeit small) populations of *Scabiosa canescens* within a distance of < 100 m. *Jurinea cyanoides* (still occurring within a distance of < 100 m), which vanished on site Y, also did not re-colonize the site. In another restoration site with deep-sand "neodunes" in the "Griesheimer Sand" near Darmstadt (see Section 4.1), Weißmantel (in Storm et al. 2022) recorded a maximum dispersal distance of 13 m for *J. cyanoides*.

In their broad study of sandy old-field succession in Hungary, Albert et al. (2014) found that there is generally a clear limitation to the establishment of target species without inoculation, especially if the surrounding species pool is small. However, in our case, the directly adjacent nature protection and reference site S was rich in target species (on average 21 species at three plots). This is in line with the results of Kiehl & Pfadenhauer (2007) in dry grassland near Munich; the authors found hardly any spontaneous colonization by target species of a restoration site in the direct vicinity of a reference site. In landscapes with virgin steppe sites in southern Ukraine, it is supposed that on former arable fields, the spontaneous re-establishment of steppe plant species needs about 100 years or more (Dembisz et al. 2023).

The corridor provides insights into the general **course of development on bare ground**. Due to inoculation and seed rain, the number of all species was already quite high in the 1st year. It took 5 (R plots) or 11 (Y plots) years to reach a peak of phytodiversity. The peak years represent a transition from the initial to the later stages of development, with some *Stellarietea* species still present and an increasing number of *Koelerio-Corynephoretea* and *Festuco-Brometea* species. Consequently, phytodiversity has declined since that time. In contrast, the sum of species cover started at 1% in the initial year, and a preliminary peak was apparent only in the last year of our study. Even in this year, the area of open soil exceeded that of the reference sites. It can be concluded that the processes of development observed are markedly different in terms of species diversity and vegetation cover. The quantitative re-vegetation of the open soil is a long-term process that is dependent on the prevailing abiotic conditions and the current grazing management regime, which aims to maintain a certain level of open soil.

The pioneer stage of development was characterized by *Stellarietea* species and lasted about 3 years (Section 3.4.3). This can also be inferred from the vector indicating the number of species in that class in the ordination graph and the DCA graph showing the estimated species optima. In the last years, there was again a small window of higher cover of one *Stellarietea* species, built up by *Bromus tectorum.* This annual species (with the relatively low Ellenberg nutrient value of 4) is classified as a *Stellarietea* species, but it overlaps into *Corynephoretalia* communities (Oberdorfer 2001). It shows higher cover percentages, especially after wet spring periods (as in 2023). The probable origin of the diaspores of *Stellarietea* species is likely the seed rain. In our area, this path was studied directly adjacent to the south of the corridor on an older restoration site (Fig. 3, bottom; Stroh et al. 2002, 2007) and showed the high importance of *Erigeron canadensis*. In 2005 (construction of the corridor) and in later years, this species was still frequent on this site in the neighborhood. Regarding the species numbers and cover, a first stage of mostly annual *Stellarietea* species, especially *Erigeron canadensis*, was present in the R and Y plots.

In the subsequent stage of development, ruderal species belonging to the *Agropyretea* or *Artemisietea* classes contributed to some extent to the cover of vegetation, yet they never achieved dominance, either in terms of species diversity or vegetation cover, and vanished by the preliminary end of the study. Instead, target species of the classes *Koelerio-Corynephoretea* (*KC*), *Festuco-Brometea* (*FB*), and transition types (*KC/FB*) were absolutely dominant (proportion > 50%) in the R and Y plots since the 2nd year (or 3rd year) with respect to number and cover. Most of them had been transferred by the inoculated plant material, but seed-bank species, too, can be transferred by the transfer of soil particles (by raking technique). According to the investigations by Krolupper & Schwabe (1998) in the adjacent target site S, *Arenaria serpyllifolia* agg., *Cerastium semidecandrum*, and *Silene otites* showed higher numbers in the seed bank of the upper soil (1–6 cm) and were all present in the corridor from the 1st to 2nd year until the last year. Nevertheless, the seed bank as a donor in situ often has very limited importance, especially on deep sand or eroded substrates, as also stated for calcareous alpine grasslands by Wellstein et al. (2024).

According to the DCA graph, the speed of species change decelerated markedly in recent years. The trajectories exhibit only minimal fluctuations, comparable to the inter-annual variations at the reference sites. This indicates a stabilization of the achieved restoration success. Compared to the older restoration plots (R), the younger plots (Y) developed even faster. They were situated within an intact *Koelerion glaucae* environment, in contrast to the R plots, which were initially surrounded by bare ground and former fields.

Other studies show that regarding the species numbers of *Stellarietea* species, the results are quite similar to those of the first 3 years of the succession experiment on a former field in the "Neuer Botanischer Garten der Universität Göttingen" (Schmidt 1993) and are also similar to the results of a summarizing study on old-field succession in Central Europe (3–5 years: Prach & Pyšek 2001). For a restoration experiment on a former field in the Darmstadt area, the results are similar regarding the number of *Stellarietea* species (first 4 years) and regarding the dominance of *KC, KC/FB,* and *FB* vegetation after 5 years (Storm et al. 2022). Longer stages with herbaceous or graminoid perennials of the *Artemisietea* and *Agropyretea* classes (subsequently following the *Stellarietea* stage), as described for old-field successions (Schmidt 1993, Prach & Pyšek 2001), were to a great extent suppressed in our site by inoculation and grazing (Stroh et al. 2002), nutrient-poor conditions, and the "environmental filtering" of the site characteristics, which Mudrák et al. (2023), too, listed as an important factor for the restoration of species-rich grasslands. In an older restoration site (richer in soil phosphate than our site) in the vicinity (Fig. 3, bottom), the cover of *Calamagrostis epigejos* was after 10 years lower than 10–15% after inoculation and successive sheep and donkey grazing; in the case of spontaneous succession, the cover was between 50% and 60% (Stroh et al. 2007). In general, the stress-tolerators (in our case of the classes *KC* and *FB*) gained more and more importance, as was also shown by Krickl & Poschlod (2023) for a 25-year period of restored and grazed calcareous dry grassland next to a reference site.

4.3 Can we use the target-species ratio (TSR) as a synoptic value for different plot sizes, also compared with other pioneer and grassland vegetation types?

The TSR values of the R and Y plots (very similar for the smaller plot sizes), between 0.7 and nearly 0.8 for TSR_{quant} and between 0.6 and 0.7 for TSR_{qual}, are outstanding. They are much higher than those of the recognized nature reserve “Griesheimer Düne und Eichwäldchen”: 0.4–0.5 (TSR_{qual}) and 0.5–0.6 (TSR_{quant} in the later years) at 79 m^2 plots (Schwabe et al. 2013). One of our grazed permanent plots (25 m^2), with relatively open *Koelerion glaucae/Allio-Stipetum* vegetation, in the area “Griesheimer Düne” reached 0.7 to nearly 0.9 (data from 22 years, TSR_{quant}). The TSR_{qual} in the grazed plot was 0.6 and 0.7 in the last years (comparable to the values of the small R plots in this study) (Schwabe et al. 2024).

If the absolute number of target species is considered, analogous results are obtained. A number of 20–23 (R plots) or 14–18 (Y plots) target species is not only similar to the number of target species in our reference plots but also to a range of 14–20 target species at grazed plots (79 m^2, sheep, donkeys, 12 years, 14 plots) in the protected area “Griesheimer Düne” west of Darmstadt (*Allio-Stipetum* with *Koelerion glaucae* elements; Schwabe et al. 2013).

In other nutrient-poor communities, for example those of the *Nardo-Callunetea* class in southwestern Germany (Black Forest), the TSR_{qual} reached a maximum of 0.6 but was mostly only about 0.4 to 0.5. Historical data from 1946 show a value of 0.8 (Schwabe & Kratochwil 2021, 2022). In contrast to the variables that are sensitive to plot size, the TSR curves exhibit a high degree of similarity, indicating that TSR as a ratio is robust to plot size and therefore suitable as a reliable indicator of restoration success. The TSR represents a synoptic value with generally high comparability between plot types, plot sizes, and different community types of a broad habitat range.

The TSR can be calculated not only for plants but also for other taxonomic groups. Krausch (2011) studied the wild-bee fauna (*Hymenoptera Anthophila*) of the corridor for the first 5 years, using our plot system, and recorded the development of a rich bee fauna with many target species of sandy habitats. The TSR_{quant} values had a maximum of about 0.4, and the TSR_{qual} was about 0.3, similar to or even higher than the values of the reference sites in the vicinity. As in all biodiversity approaches, comparisons must be taxon specific, and bee data are not comparable with our plant TSR data.

4.4 Was there an impact of extreme heat/drought years?

Such events can affect vegetation, even though sand vegetation is adapted to such stressors. In a longtime study of *Allio-Stipetum* vegetation (partly with *Koelerion glaucae* elements) in the area “Griesheimer Düne” west of Darmstadt (including all years of the corridor study), we detected severe declines in annual species in years with extreme heat/drought (2011, 2015, 2018, and 2022) (see Fig. 14 and Schwabe et al. 2024). Such annual species are typical elements of the *Koelerio-Corynephoretea* class and are partly red-listed or nearly-threatened (e.g., *Phleum arenarium*, *Medicago minima*, *Silene conica*, *Vicia lathyroides*).

In the corridor relevés, no pronounced declines in annuals in the years with extreme weather were found. In comparison to the restoration site, the “Griesheimer Düne” and the “Ehemaliger August-Euler-Flugplatz” are large (> 40 ha) nature reserves. The Griesheimer Düne plots are situated in a very open landscape in the western, northern, and eastern directions (Schwabe et al. 2024; Fig. 2a). The vicinity of the "Ehemaliger August-Euler-Flugplatz" is predominantly characterized by large agricultural fields to the west and south. The forest patches are small and fragmented (Storm et al. 2019; Fig. 1). In contrast, the corridor is situated in a landscape complex with *Pinus sylvestris* forest in the western direction, single *Pinus sylvestris* specimens (mainly shrubs and in 2023 also some young trees) on the margin of the corridor, and mainly sandy vegetation in a complex with pine forest in the northern, eastern, and southern directions. The corridor appears to be less exposed to the impacts of the strong heat and drought than the other areas.

5. Conclusions

Restoration is an important target for the global agenda in the frame of the UN Decade on Ecosystem Restoration 2021–2030 (Wellstein et al. 2024). From a global perspective open ecosystems have been particularly neglected (Török et al. 2021, Barbosa-Dias et al. 2024).

Our findings demonstrate that restoration approaches are the only means of expanding the area of the highly endangered pioneer stages of subcontinental sandy vegetation with their endangered plant species, as observed in our area. Long-term monitoring has demonstrated that the processes of development exhibited varying rates of progression, with some occurring rapidly and others taking longer. After 19 years, the indicators of restoration success reached the benchmark of the reference sites, as well as that of other reference areas in the region. Monitoring has to be long-term and may otherwise lead to wrong conclusions about the impact of management techniques (Török et al. 2021).

The use of donkeys for grazing management has proven to be an effective method for maintaining the desired restoration results thus far. Grazing should be applied at low intensity, which had also been shown for restored nutrient-poor montane grassland by Helbing et al. (2023), not only regarding the vegetation, but also different groups of arthropods. It is imperative to maintain the success of our restoration project by pursuing a management strategy that ensures dynamic processes between the current state and slight successional and regression processes. This will ensure the long-term persistence of a diverse pattern of *Koelerion glaucae* and *Allio-Stipetum* vegetation.

Erweiterte deutsche Zusammenfassung

Einleitung – In der gesamten EU gehören trockene basenreiche Binnenland-Sandrasen zu den extrem gefährdeten Habitattypen; dies gilt insbesondere für das *Jurineo cyanoidis-Koelerietum glaucae* Volk 1931 (Verband *Koelerion glaucae* Volk 1931). Dieser Habitattyp ist als gefährdet in der Fauna-Flora-Habitat Richtlinie (FFH) mit dem Code 6120 gelistet (European Commission 2013). Zu den seltenen Pflanzenarten gehören u. a. *Alyssum gmelinii*, *Bassia laniflora*, *Fumana procumbens*, *Jurinea cyanoides*, *Koeleria glauca* und *Poa badensis*. In der nördlichen Oberrheinebene in Südhessen gab es in den 1990er Jahren nur noch kleinere fragmentierte Restflächen in wenigen geschützten Gebieten. Hauptursachen für den dramatischen Rückgang sind Vergrößerungen von Siedlungen, landwirtschaftliche Nutzung, Aufforstungen, Rückgang der Sanddynamik in den kleinen Restflächen, Eutrophierung, spontane Sukzession u. a. Dies konnte auch für andere Sandlebensräume in Europa aufgezeigt werden (z. B. Kooijman & van der Meulen 1996, Wiesbauer et al. 1997, Kollmann 2019).

Inzwischen sind in Südhessen umfangreiche Restitutionsmaßnahmen zur Re-Etablierung von Sandrasen durchgeführt worden. Wir berichten hier über ein Modell-Restitutionsgebiet in Seeheim-Jugenheim (südlich von Darmstadt), dessen Entwicklung bereits für die ersten 10 Jahre in dieser Zeitschrift vorgestellt wurde (Storm et al. 2016). Mittlerweile konnte die Entwicklung für 19 Jahre analysiert werden; hinzu kommt eine Erweiterungsfläche („Neodüne“), deren Entwicklung über 15 Jahre untersucht wurde. Der aufgeschüttete nährstoffarme Tiefensand-Korridor zwischen zwei Sandlebensräumen (Abb. 3) wurde in einem Drei-Stufen-Ansatz restituiert: 1. Abiotisch: Aufschüttung von basenreichem Tiefensand; 2. biotisch: Inokulation von Pflanzenmaterial mit Diasporen aus gut entwickelten Spenderflächen und 3. Management mit extensiver Eselbeweidung.

Ziel war die erfolgreiche längerfristige Etablierung von *Koelerion glaucae*-Vegetation mit den entsprechenden Zielarten, erhalten durch die Eselbeweidung, die auch Ruderalisierungen unterdrückt.

Methoden – Wir führten jährliche pflanzensoziologische Aufnahmen in einem geschachtelten Ansatz mit zwei Größen (25 m^2, 79 m^2) auf 9 kreisförmigen Plots durch über 19 Jahre (6 R-Plots) und auf der „Neodüne“ 15 Jahre (3 Y-Plots). Wir analysierten die Daten mit einer Stetigkeitstabelle, mit Ordinationsmethoden, Klassifikation sowie mit Berechnungen verschiedener struktureller Eigenschaften und Diversitätsmerkmale, darunter mit der Zielarten-Ratio (target-species ratio: TSR, qualitativ und quantitativ).

Ergebnisse – Es zeigte sich, dass bis zum letzten Untersuchungsjahr (Y-plots: nach 15 Jahren und R-plots: sogar nach 19 Jahren) die *Koelerion glaucae*-Vegetation sehr gut entwickelt war und viele Rote Liste-Arten (einschließlich Arten der Vorwarnliste) aufwies.

Die Entwicklung begann mit einer *Stellarietea mediae*-Phase, die von der zunehmenden Dominanz von Arten der *Koelerio-Corynephoretea* und *Festuco-Brometea* abgelöst wurde. Die Phytodiversität erreichte den Höhepunkt nach 5–11 Jahren, verbunden mit einer steten Erhöhung der Vegetationsdeckung. In den letzten Jahren erreichte die Entwicklung Verhältnisse mit schwächerer Dynamik. Leichte Veränderungen traten auf, angezeigt durch einige Arten der *Festuco-Brometea* und Zunahme von Moosen. Ruderalisierungsprozesse konnten weitgehend unterdrückt werden.

Der Vergleich der älteren R-Plots und der jüngeren Y-Plots zeigt bemerkenswerte Ähnlichkeiten der Trajektorien der Entwicklung. Es ist bemerkenswert, dass die initiale floristische Struktur (moduliert durch Diasporen von der jeweiligen Spenderfläche) sich nicht vollkommen ausgeglichen hat im Laufe der Jahre (dies weist auf Diasporen-Limitation hin).

Die Zielarten-Ratio (TSR_{qual}) wies die höchsten Werte am Ende des Untersuchungszeitraums auf, wohingegen TSR_{quant} und Rote Liste-Arten (einschließlich Arten der Vorwarnliste) diesen Peak früher erzielten. Alle Werte erreichten die Benchmark der Referenzflächen (gleichzeitig Donor-Flächen).

Die verwendeten Plot-Größen zeigten bei den kleineren Plots eine Reduzierung der Artenzahl (spätere Jahre: ca. 80–90 % der Arten der großen Plots wurden erfasst); bei den größeren Plots reduzierten sich die Effekte des stochastischen punktuellen Absterbens von Pflanzenarten. Wie erwartet wird der TSR-Wert als synoptisches Maß kaum durch die Plotgröße beeinflusst.

Diskussion – In älteren Binnendünen-Komplexen gelang es kaum, durch Beweidung Bestände des *Koelerion glaucae* zu vergrößern, wie unsere Langzeit-Untersuchungen im „Griesheimer Sand“ bei Darmstadt gezeigt haben (Schwabe et al. 2024). Die Restitution auf Tiefensand zeigte jedoch im Zuge des Drei-Stufen-Ansatzes hervorragende Ergebnisse für einen Zeitraum von 19 Jahren. Auch Tischew et al. (2017) betonen, dass für die Wiedereinbringung z. B. von *Jurinea cyanoides* eine drastische Behandlung des Substrates notwendig ist, indem im Falle dieser Studie der Oberboden entfernt wurde. *Jurinea cyanoides* etablierte sich im Korridor nur eine kürzere Zeitperiode, war jedoch auf Tiefensand in einer anderen Restitutionsfläche im „Griesheimer Sand“ seit 12 Jahren erfolgreich auf drei von unseren Untersuchungsflächen etabliert worden (Storm et al. 2022). Die gefährdeten Arten *Alyssum gmelinii*, *Bassia laniflora*, *Euphorbia seguieriana*, *Fumana procumbens*, *Koeleria glauca*, *Phleum arenarium*, *Silene conica*, *S. otites* u. a. bildeten jedoch große Populationen über viele Jahre. Ohne Inokulation gibt es klare Limitationen im Erfolg der Restitution, wie auch von ähnlichen Systemen berichtet wird (z. B. für aufgelassene Sandäcker in Ungarn: Albert et al. 2014). Das Monitoring muss langzeitig durchgeführt werden; anderenfalls kann man bei zu kurzen Zeitperioden falsche Schlüsse zur Wirkung der Management-Maßnahmen ziehen (siehe auch Török et al. 2021).

In Jahren mit Hitzewellen und großer Trockenheit konnten wir in anderen Untersuchungsflächen (im sehr offenen und exponierten „Griesheimer Sand“ bei Darmstadt) in den letzten knapp 20 Jahren starke Rückgänge von Annuellen (die oft zu den gefährdeten *Koelerio-Corynephoretea*-Arten gehören) feststellen (Schwabe et al. 2024). Diese Reaktionen waren auf dem Korridor in einem weniger exponierten und weniger offenen Landschaftsausschnitt nur gemäßigt.

Es ist notwendig, dass das Beweidungsmanagement mit Eseln gesichert bleibt, um das vielfältige Mosaik der vorwiegend durch das *Koelerion glaucae* geprägten Vegetation zu erhalten. Der bisherige Erfolg des Restitutionsprojektes war außerordentlich hoch und kann als Modell für die Praxis der Wiederherstellung dieses schwindenden Habitattyps dienen.

Acknowledgements

We are grateful to the German Federal Ministry for Environment, Nature Conservation and Nuclear Safety, the German Federal Agency for Nature Conservation, and the Landkreis Darmstadt-Dieburg for financial and logistic support of our longtime study (a project of the Technische Universität Darmstadt, Biology, Vegetation and Restoration Ecology). The inoculation and donkey grazing were, with great expert knowledge, managed by Landschaftspflegehof Stürz. We thank the Associate Editor and two anonymous reviewers for valuable suggestions improving the manuscript.

Author contribution statement

AS and CS performed the design, supervised the data collection, analyzed the data, and wrote the manuscript. MS sampled all data of the restoration plots and the T reference/donor plots, and AS sampled the data of the S reference/donor plots. All authors were involved in the implementation and compilation of management practices and checked the final version of the manuscript.

ORCID iDs

Christian Storm https://orcid.org/0000-0001-9662-8131
Angelika Schwabe https://orcid.org/0000-0003-0698-5763

Supplements

Supplement S1. Constancy table of six plots (%) 2005 to 2023 (R1–R6: older restoration site) and three plots 2009 to 2023 in absolute values (Y1–Y3: younger restoration site).

Beilage S1. Stetigkeitstabelle von sechs Plots (%) 2005 to 2023 (R1–R6: ältere Restitutionsfläche) und drei Plots 2009 to 2023 in absoluten Werten (Y1–Y3: jüngere Restitutionsfläche).

Additional supporting information may be found in the online version of this article.

Zusätzliche unterstützende Information ist in der Online-Version dieses Artikels zu finden.

Supplement E1. Detrended correspondence analysis (DCA) as in Figure 4, based on the rank-transformed Braun-Blanquet data of the large plots.

Anhang E1. Detrended Correspondence Analysis (DCA) wie in Abbildung 4 für die rangtransformierten Daten der großen Plots.

Supplement E2a. Detrended correspondence analysis (DCA) as Figure 4, but with species shown instead of plots.

Supplement E2a. Detrended Correspondence Analysis (DCA) wie in Abbildung 4, aber mit Darstellung der Arten anstelle der Plots.

Supplement E2b. Species abbreviations in E2a.

Anhang E2b. Abkürzungen der Arten in E2a.

Supplement E3. Mean number of target species in comparison to all species of the large restoration plots over the course of the study period.

Anhang E3. Mittlere Zielartenzahlen im Vergleich zu den Gesamtartenzahlen der großen Restitutions-Plots im Verlauf der Untersuchungsperiode.

Supplement E4. Mean target species ratios (TSR) of the large restoration plots in comparison to the small plots over the course of the study period.

Anhang E4. Mittlere Zielarten-Ratios (TSR) der großen Restitutions-Plots im Vergleich zu den kleinen Plots im Verlauf der Untersuchungsperiode.

References

AG Boden (Bundesanstalt für Geowissenschaften und Rohstoffe) (2005): Bodenkundliche Kartieranleitung. 5. Aufl. – Schweizerbart, Stuttgart: 392 pp.

Albert, A.-J., Kelemen, A., Valkó O. … Török, P. (2014): Secondary succession in sandy old-fields: a promising example of spontaneous grassland recovery. – Appl. Veg. Sci. 17: 214–224. https://doi.org/10.1111/avsc.12068

Barbosa-Dias, L.D., Silveira, F.A.O., De Marco junior, P. & Padilha, D.L. (2024): Open ecosystems restoration: a global review shows biases and mismatches between theory and practice. – Restor. Ecol. https://doi.org/10.1111/rec.14307

Beil, M., Kratochwil, A., Storm, C. & Schwabe, A. (2014): Community structure and diversity of vegetation and flower-visiting wild bees (*Hymenoptera*: *Apoidea*) in sandy dry grassland: are there congruent characteristics? – Phytocoenologia 44: 175–192. https://doi.org/10.1127/0340-269X/2014/0044-05887

Caspari, S., Dürhammer, O., Sauer, M. & Schmidt, C. (2018): Rote Liste und Gesamtartenliste der Moose (*Anthocerotophyta* und *Bryophyta*). – Naturschutz Biolog. Vielfalt 70: 361–489.

Dahlgren, J., Bengstsson, K. & Ehrlén, J. (2016): The demography of climate-driven and density-regulated population dynamics in a perennial plant. – Ecology 97: 899–907. https://doi.org/10.1890/15-0804.1

Dembicz, I., Zachwatowicz, M., Moysiyenko, I. … Sudnik-Wójcikowska, B. (2023): Rapid functional but slow species diversity recovery of steppe vegetation on former arable fields in southern Ukraine. – Appl. Veg. Sci. 26. e12756. https://doi.org/10.1111/avsc.12756

Durbecq, A., Rocher, L., Jaunatre, R. … Bischoff, A. (2022): Mountain grassland restoration using hay and brush material transfer combined with temporary wheat cover. – Ecol. Eng. 174: 106447. https://doi.org/10.1016/avsc.12756/j.ecoleng.2021.106447

Egler, F.E. (1954): Vegetation science concepts. I. Initial floristic composition, a factor in old-field vegetation development. – Vegetatio 4: 412–417. https://doi.org/10.1007/BF00275587

Eichberg, C., Storm, C. & Schwabe, A. (2005): Epizoochorous and post-dispersal processes in a rare plant species: *Jurinea cyanoides* (L.) Rchb. (*Asteraceae*). – Flora 200: 477–489. https://doi.org/10.1016/j.flora.2005.02.005

Eichberg, C., Storm, C., Stroh, M. & Schwabe, A. (2010): Is the combination of topsoil replacement and inoculation with plant material an effective tool for the restoration of threatened sandy grassland? – Appl. Veg. Sci. 13: 425–438. https://doi.org/10.1111/j.1654-109X.2010.01082.x

Ernst, M. (2017): Tagfaltermonitoring Transektstrecke "Seeheimer Düne“ (HE-6217-3), vergleichende Ergebnisse aus den Jahren 2006–2015. – Oedippus 33: 16–29.

European Commission (2013): Interpretation Manual of European Union Habitats, EUR 28. – European Commission, DG Environment, Brussels. – URL: https://eunis.eea.europa.eu/references/2435 [accessed 2024-06-19].

Gilhaus, K., Vogt, V. & Hölzel, N. (2015): Restoration of sand grasslands by topsoil removal and self-greening. – Appl. Veg. Sci. 18: 661–673. https://doi.org/10.1111/avsc.12176

Helbing, F., Fartmann, T., Morkel, C. & Poniatowski, D. (2023): Rapid response of vascular Plants and insects to restoration of montane grasslands. – Frontiers Ecol. Evol. 11: 1148266. https://doi.org/10.3389/fevo.2023.1148266

HLNUG (Hessisches Landesamt für Naturschutz, Umwelt und Geologie) Bearb. Vogt-Rosendorff, C., Fritsch, M. & Böger, K. (2022): Artgutachten 2022. Bundesmonitoring 2022 der Sand-Silberscharte (*Jurinea cyanoides*). – Gießen: 77 pp.

Hofmann, S., Conradi, T., Kiehl, K. & Albrecht, H. (2020): Effects of different restoration treatments on long-term development of plant diversity and functional trait composition in calcareous grasslands. – Tuexenia 40: 175–200. https://doi.org/10.14471/2020.40.006

Hodvina, S. & Cezanne, R. (2007a): *Fumana procumbens* in Hessen. – Bot. Naturschutz Hessen 19: 43–67.

Hodvina, S. & Cezanne, R. (2007b): Das Dünen-Steinkraut (*Alyssum montanum* subsp. *gmelinii*) in Hessen. – Bot. Naturschutz Hessen 20: 25–51.

Hodvina, S. & Cezanne, R. (2008): Das Badener Rispengras (*Poa badensis*) in Hessen. – Bot. Naturschutz Hessen 21: 33–60.

Hölzel, N., Buisson, E. & Dutoit, T. (2012): Species introduction – a major topic in vegetation restoration. – Appl. Veg. Sci. 15: 161–165. https://doi.org/10.1111/j.1654-109X.2012.01189.x

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. https://doi.org/10.1111/j.1654-109X.2003.tb00573.x131-140

Jäger, E.J. (Ed.) (2017): Rothmaler – Exkursionsflora von Deutschland. Gefäßpflanzen. Grundband. 21. Aufl. –Springer Spektrum, Berlin: 930 pp.

Ketner-Oostra, R., Aptroot, P., Jungerius, P.D. & Sýkora, K.V. (2012): Vegetation succession and habitat restoration in Dutch lichen-rich inland drift sands. – Tuexenia 32: 245–268.

Kiehl, K., Kirmer, A., Donath T., 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. https://doi.org/10.1016/j.baae.2010.02.008

Kiehl, K. & Pfadenhauer, J. (2007): Establishment and long-term persistence of target species in newly created calcareous grasslands on former arable fields. – Plant Ecol. 189: 31–48. https://doi.org/10.1007/s11258-006-9164-x

Klinkovská, K., Sperandii, M.G. Trávníček, B. & Chytrý, M. (2024): Significant decline in habitat specialists in semi-dry grasslands over four decades. – Biodiv. Conserv. 33: 161–178. https://doi.org/10.1007/s10531-023-02740-6

Koerner, S.E., Smith, M.D., Burkepile, D.E. … Zelikova, T.J. (2018): Change in dominance determines herbivore effects on plant diversity. – Nature Ecol. & Evol. 2: 1925–1932. https://doi.org/10.1038/s41559-018-0696-y

Kollmann, J. (2019): Sandrasen. – In: Kollmann, J., Kirmer, A., Tischew, S., Hölzel, N. & Kiehl, K. (Eds.): Renaturierungsökologie: 311–328. Springer Spektrum, Berlin.

Kooijman, M. & van der Meulen, F. (1996): Grazing as a control against "grass-encroachment" in dry dune grasslands in the Netherlands. – Landsc. Urban Plan. 34: 323–333. https://doi.org/10.1016/0169-2046(95)00225-1

Korneck, D. (1974): Xerothermvegetation in Rheinland-Pfalz und Nachbargebieten. –Schriftenr. Vegetationskd. 7: 1–196.

Krausch, S. (2011): E+E-Vorhaben "Ried und Sand": Erfolge bei der Restitution von Sandlebensräumen für Wildbienen. – In: Süß, K., Storm, C. & Schwabe, A. (Eds.): Ried und Sand: Biotopverbund und Restitution durch extensive Landbewirtschaftung. – Naturschutz Biol. Vielfalt 110: 215–234.

Krickl, P. & Poschlod, P. (2023): Calcareous grassland restored by clearance and subsequent sheep grazing show fast recovery of plant functional traits – Results from a 25-year-long experiment. – Global Ecol. Conserv. 45: e02509. https://doi.org/10.1016/j.gecco

Krolupper, N. & Schwabe, A. (1998): Ökologische Untersuchungen im Darmstadt-Dieburger Sandgebiet (Südhessen): Allgemeines und Ergebnisse zum Diasporen-Reservoir und -Niederschlag. – Bot. Naturschutz Hessen 10: 9–39.

Krumbiegel, A., Brade, P., Eckstein, J., Glowka, B., Hein, C., Meysel, F. & Müller, F. (2022): Zehn Jahre Monitoring der FFH-Pflanzenarten der Anhänge II und IV in Sachsen-Anhalt – eine Zwischenbilanz. – Mitt. florist. Kart. Sachsen-Anhalt 27: 3–65.

Lamoot, I., Callebaut, J., Demeulenaere, E., Vandenberghe, C. & Hoffmann, M. (2005): Foraging behaviour of donkeys grazing in a coastal dune area in temperate climate conditions. – Appl. Anim. Behav. Sci 92: 93–112. https://doi.org/10.1016/j.applanim.2004.10.017

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

Metzing, D., Garve, E. & Matzke-Hajek, G. (2018): Rote Liste und Gesamtartenliste der Farn- und Blütenpflanzen (Tracheophyta) Deutschlands. – Naturschutz Biol. Vielfalt 70: 13–358.

Mudrák, O., Jongepierová, I., Řehounková, K. & Prach, K. (2023): Large-scale restoration of species-rich dry grasslands on arable land: Environmental filtering drives successful species establishmant over a period of 10 years. – J. Appl. Ecol. 60:1893–1903. https://doi.org/10.1111/1365-2664.14456

Oberdorfer, E. (2001): Pflanzensoziologische Exkursionsflora für Deutschland und angrenzende Gebiete. 8. Aufl. – Ulmer, Stuttgart: 1051 pp.

Otýpková, Z. & Chytrý, M. (2006): Effects of plot size on the ordination of vegetation samples. – J. Veg. Sci. 17: 465–472. https://doi.org/10.1111/j.1654-1103.2006.tb02467.x

Plenk, K., Bardy, K., Höhn, M. & Kropf, M. (2019): Long-term survival and successful conservation? Low genetic diversity but no evidence for reduced reproductive success at the north-westernmost range edge of *Poa badensis* (*Poaceae*) in Central Europe. – Biodiv. Conserv. 28: 1245–1265. https://doi.org/10.1111/j.1654-1103.2006.tb02467.x

Prach, K. & Pyšek, P. (2001): Using spontaneous succession for restoration of human-disturbed habitats: experience from Central Europe. – Ecol. Eng. 17: 55–62. https://doi.org/10.1016/S0925-8574(00)00132-4

Riksen, M., Kentner-Oostra, R., van Turnhout, C. … Spaan, W. (2006): Will we lose the last active inland drift sands of Western Europe? The origin and development of the inland drift-sand ecotype in the Netherlands. – Landsc. Ecol. 21: 431–447. https://doi.org/10.1007/s10980-005-2895-6

Schmidt, W. (1993): Sukzession und Sukzessionslenkung auf Bracheäckern. Neue Ergebnisse aus einem Dauerflächenversuch. – Scr. Geobot. 20: 65–104.

Schwabe, A., Cezanne, R., Eichler, M. & Storm, C. (2024): Kontinuierliche Dauerflächen-Untersuchungen in beweideten und unbeweideten Sandrasen und ihren Gebüschstadien im Naturschutzgebiet „Griesheimer Düne und Eichwäldchen“ (Südhessen) in bis zu 23 Vegetationsperioden.– Bot. Naturschutz Hessen 36: 119–163.

Schwabe, A. & Kratochwil, A. (2021): Montane Borstgrasrasen (*Festuco-Genistelletum sagittalis*) im südlichen Schwarzwald: Veränderungen einer gefährdeten Pflanzengemeinschaft in den letzten 40 Jahren. – Ber. Naturforsch. Ges. Freiburg i. Br. 110/111: 337–411.

Schwabe, A. & Kratochwil, A. (2022): Hochmontane Borstgrasrasen (*Leontodonto-Nardetum*) im Schwarzwald: Entstehung, Bewirtschaftung und Veränderungen der floristischen Struktur in den letzten 40 Jahren –Tuexenia 42: 201–244. https://doi.org/10.14471/2022.42.003

Schwabe, A., Storm, C., Zeuch, M. Kleine-Weischede, H. & Krolupper, N. (2000): Sandökosysteme in Südhessen: Status quo, jüngste Veränderungen und Folgerungen für Naturschutz-Maßnahmen. – Geobot. Kolloqu. 15: 25–45.

Schwabe, A., Süß, K. & Storm, C. (2013): What are the long-term effects of livestock grazing in steppic sandy grassland with high conservation value? Results from a 12-year field study. – Tuexenia 33: 189–212.

Ssymank, A., Hauke, U., Rückriem, C. & Schröder, E. (1998): Das europäische Schutzgebietssystem NATURA 2000. BfN-Handbuch zur Umsetzung der Fauna-Flora-Habitat-Richtlinie (92/43/EWG) und der Vogelschutzrichtlinie (79/409/EWG). – Schriftenr. Landschaftspfl. Naturschutz 53: 1–558.

Storm, C., Cezanne, R., Eichler, M. & Schwabe, A. (2019): Multi-stress-affected sandy grasslands: Livestock-grazing as a tool for nature conservation under the impact of drought events and rabbit population fluctuations? – Tuexenia 39: 215–248. https://doi.org/10.14471/2019.39.004

Storm, C., Cezanne, R., Eichler, M. … Schwabe, A. (2022): Restitution von Sandrasen auf ehemaligen Äckern durch Inokulation und Beweidung – eine 16jährige Modellstudie aus Südhessen. – Bot. Naturschutz Hessen 34: 67–114.

Storm C., Eichberg, C., Stroh, M. & Schwabe, A. (2016): Restoration of steppic sandy grassland using deep-sand deposition, inoculation with plant material and grazing: a 10-year study. – Tuexenia 36: 143–166. https://doi.org/10.14471/2016.36.010

Stroh, M. (2006): Vegetationsökologische Untersuchungen zur Restitution von Sand-Ökosystemen. – Thesis, Technische Universität Darmstadt: 125 pp. and supplement.

Stroh, M., Storm, C. & Schwabe, A. (2007): Untersuchungen zur Restitution von Sandtrockenrasen: das Seeheim-Jugenheim-Experiment in Südhessen (1999–2005). – Tuexenia 27: 287–305.

Stroh, M., Storm, C., Zehm, A. & Schwabe, A. (2002): Restorative grazing as a tool for directed succession with diaspore inoculation: the model of sand ecosystems. – Phytocoenologia 32: 595–625. https://doi.org/10.1127/0340-269X/2002/0032-0595

Süß, K. & Schwabe, A. (2007): Sheep versus donkey grazing or mixed treatment: results from a 4-year field experiment in Armerio-Festucetum trachyphyllae sand vegetation. – Phytocoenologia 37: 135–160. https://doi.org/10.1127/0340-269X/2007/0037-0135

Süß, K., Storm, C. & Schwabe, A. (2010): Sukzessionslinien in basenreicher offener Sandvegetation des Binnenlandes – Ergebnisse aus Untersuchungen von Dauerbeobachtungsflächen. – Tuexenia 30: 289–318.

Thiv, M., Gerth, A. & Meierott, L. (2022): *Alyssum montanum* l. oder A. gmelinii Jord. & Fourr.? Der Komplex des Berg-Steinkrauts (*Brassicaceae*) in Süd- und Ostdeutschland. – Ber. Bayer. Bot. Ges. 92: 5–13.

Timmermann, A., Damgaard, C., Strandberg, M.T. & Svenning, J.-C. (2015): Pervasive early 21st-century vegetation changes across Danish semi-natural ecosystems: more losers than winners and a shift towards competitive, tall-growing species. – J. Appl. Ecol. 52: 21–30. https://doi.org/10.1111/1365-2664.12374

Tischew, S., Kommraus, F., Fischer, L.K. & Kowarik, I. (2017): Drastic site-preparation is key for the successful reintroduction of the endangered grassland species *Jurinea cyanoides*. – Biol. Cons. 214: 88–100. https://doi.org/10.1016/j.biocon.2017.07.036

Török, P., Brudvig, L.A., Kollmann, J. … Tóthmérész, B. (2021): The present and future of grassland restoration. – Restor. Ecol. 29. e13378. https://doi.org/10.1111/rec.13378

Von Wehrden, H., Hanspach, J., Bruelheide, H. & Wesche, K. (2009): Pluralism and diversity: trends in the use and application of ordination methods 1990-2007. – J. Veg. Sci. 20: 695–705. https://doi.org/10.1111/j.1654-1103.2009.01063.x

Wellstein, C., Tónin, R., Peratoner, G. … Zerbe, S. (2024): The role of the soil seed bank for the restoration potential of eroded alpine grassland. – Rest. Ecol. 32: e14035. https://doi.org/10.1111/rec.14035

Wessels-de Wit, S. & Schwabe, A. (2010): The fate of sheep-dispersed seeds: Plant species emergence and spatial patterns. – Flora 205: 656–665. https://doi.org/10.1016/j.flora.2010.04.010

Wiesbauer, H. & Mazzucco, K. (unter Mitarbeit von Schratt-Ehrendorfer, L.) (1997): Dünen in Niederösterreich. Ökologie und Naturgeschichte eines bemerkenswerten Landschaftselementes. – Fachber. NÖ Landschaftsfonds 6/97: 1–90. St. Pölten.

Wildi, O. (2018): Evaluating the predictive power of ordination methods in ecological context. – Mathematics 6: 295. https://doi.org/10.3390/math6120295

Wirth, V., Hauck, M., von Brackel, W. … Heinrich, D. (2011): Rote Liste und Artenverzeichnis der Flechten und flechtenbewohnenden Pilze Deutschlands. – Naturschutz Biol. Vielfalt 6: 7–122.

Zech, W., Schad, P. & Hintermaier-Erhard, G. (2022): Soils of the world. – Springer, Heidelberg: 256 pp.

Supplement S1. Constancy table of six plots (%) 2005 to 2023 (R1–R6: older restoration site) and three plots 2009 to 2023 in absolute values (Y1–Y3: younger restoration site); plot size each 79 m². RL: red-listed (2, 3) and near-threatened (V) species (references, see Section 2.5), t: target species. KC: *Koelerio-Corynephoretea,* FB: *Festuco-Brometea,* St: *Stellarietea mediae,* Ag: *Agropyretea,* AgR: *Agropyretea* regional, Ar: *Artemisietea,* MA: *Molinio-Arrhenatheretea,* os: other species, ws: woody species, juv: juvenile, B: Bryophytes, L: Lichens. % data for bryophytes with partly higher cover are given if there are more than five plots.

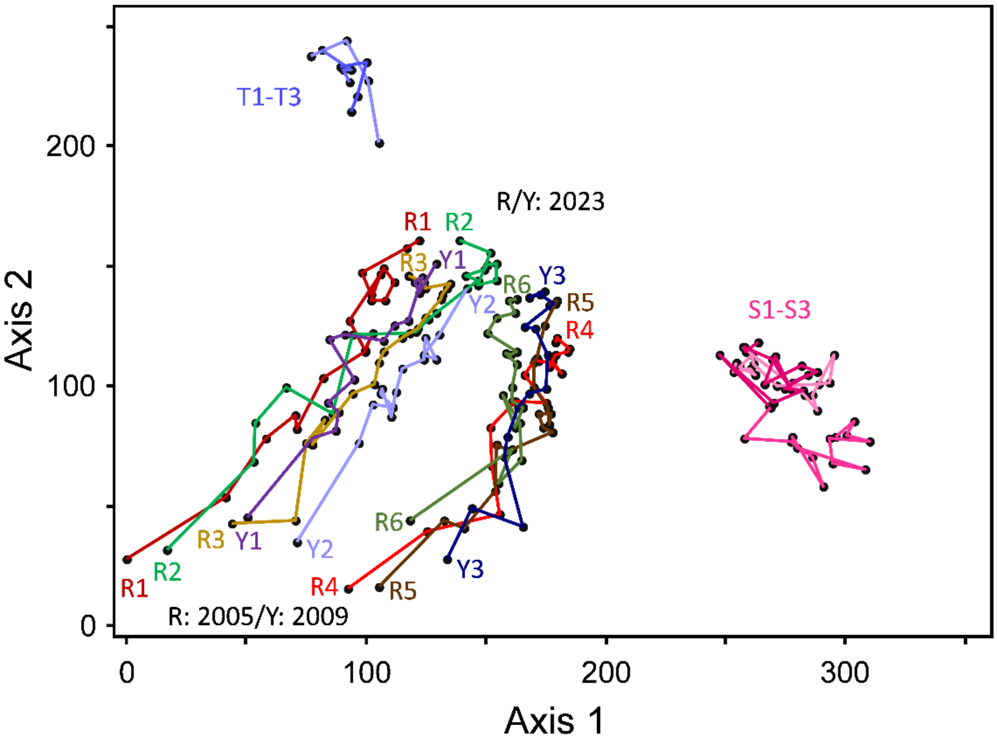
Beilage S1. Stetigkeitstabelle von sechs Plots (%) 2005 bis 2023 (R1–R6: ältere Restitutionsfläche) und drei Plots 2009 bis 2023 in absoluten Werten (Y1–Y3: jüngere Restitutionsfläche); Plotgröße jeweils 79 m2. RL: Rote Liste-Arten (2, 3) und Arten der Vorwarnliste (V) (Referenzzitate, siehe Kap. 2.5), t: Zielarten. KC: *Koelerio-Corynephoretea,* FB: *Festuco-Brometea,* St: *Stellarietea mediae,* Ag: *Agropyretea,* AgR: *Agropyretea* regional, Ar: *Artemisietea,* MA: *Molinio-Arrhenatheretea,* os: weitere Arten, ws: Gehölze, juv: juvenil, B: Moose, L: Flechten. %-Daten für Moose mit teilweise höherer Deckung sind angegeben, wenn sie mehr als fünf Flächen betreffen.

			plot numbers	older restoration site R1, R2, R3, R4, R5, R6																				younger restoration site Y1, Y2, Y3														
			running number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
			year 200., 20..	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23		9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
			open soil (%) average	99	97	92	88	84	86	81	62	53	39	31	26	22	20	14	15	11	14	13		99	97	93	80	72	62	58	50	40	30	25	25	23	25	19
			red-listed, near-threatened species (average)	1	6	8	10	12	13	13	13	13	13	14	14	15	14	14	14	13	13	13		4	7	7	8	8	8	8	8	9	9	9	9	9	8	9
	RL	t	species numbers (average)	24	33	34	36	40	39	35	35	36	37	34	36	35	34	33	31	30	31	32		19	21	21	23	24	25	24	25	26	26	27	25	25	24	23
KC		t	Arenaria serpyllifolia agg.	17	83	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	.	3	2	2	2	2	3	3	3	3	3	3	3	3	3	3
KC	V	t	Thymus serpyllum	17	33	50	67	67	67	83	83	83	83	83	83	83	83	67	83	83	67	67	.	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
KC	2	t	Alyssum gmelinii	.	67	67	83	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	.	2	1	2	3	3	3	3	3	3	3	3	3	3	3	3
KC		t	Cerastium semidecandrum	.	33	50	50	50	100	100	100	100	100	100	100	100	100	100	100	100	100	100	.	3	2	3	3	3	3	3	3	3	3	3	3	3	3	3
KC	3	t	Phleum arenarium	.	33	33	50	67	67	67	67	83	83	100	100	100	100	100	100	100	100	100	.	1	1	2	2	2	3	3	3	3	3	3	3	3	3	3
KC	2	t	Poa badensis	.	33	50	50	50	67	67	67	67	50	50	50	33	33	33	33	33	33	33	.	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
KC	3	t	Silene conica	.	67	50	67	83	100	83	83	83	100	100	100	100	100	100	100	100	100	100	.	.	2	2	1	1	.	1	1	2	2	2	2	2	2	2
KC	2	t	Bassia laniflora	.	.	17	33	33	33	50	50	50	50	17	33	33	33	50	50	50	50	50	.	2	2	2	2	2	2	1	1	1	1	1	1	1	1	1
KC	2	t	Koeleria glauca	.	.	33	33	17	50	50	50	50	50	67	67	83	100	100	100	100	100	100	.	1	1	2	3	3	3	3	3	3	3	3	3	3	3	3
KC	V	t	Medicago minima	.	67	100	100	100	100	100	100	100	100	83	100	100	100	100	83	83	50	50	.	.	2	2	2	2	2	1	1	1	1	1	1	1	.	1
KC		t	Holosteum umbellatum	.	67	50	50	50	33	33	50	83	83	50	83	83	83	83	83	83	100	100	.	.	.	.	1	2	2	.	2	2	3	3	3	3	3	3
KC		t	Corynephorus canescens	.	.	.	.	17	33	33	33	33	50	50	67	83	67	67	67	83	100	83	.	.	1	2	2	2	2	3	3	3	3	3	3	3	3	3
KC	3	t	Silene otites	.	17	50	100	50	67	67	67	67	67	83	83	83	83	83	83	83	67	83	.	.	.	.	.	.	.	2	2	2	2	2	2	2	2	2
KC		t	Echium vulgare	50	50	50	67	17	33	33	.	.	17	.	.	.	.	.	.	.	.	.	.	2	3	.	.	1	1	2	2	1	1	2	1	1	1	.
KC		t	Draba verna	.	50	.	33	17	33	33	33	67	50	33	50	17	17	17	17	17	17	17	.	.	.	.	.	1	1	.	1	.	.	.	.	.	.	.
KC		t	Trifolium arvense	.	17	33	.	33	33	17	17	17	17	17	17	17	17	17	17	17	.	50	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	1
KC		t	Vicia lathyroides	.	.	.	.	17	17	17	17	50	50	17	33	33	17	33	33	33	33	50	.	.	.	.	.	.	.	.	1	1	.	1	.	.	.	.
KC		t	Rumex acetosella	33	33	33	50	67	67	17	33	33	17	.	.	.	17	17	17	50	33	33	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KC		t	Sedum acre	83	67	50	83	83	83	33	33	33	33	33	33	33	17	17	33	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KC		t	Petrorhagia prolifera	.	17	50	50	17	50	17	17	33	33	33	.	33	50	33	.	33	33	17	.	.	.	.	.	.	.	.	.	.	1	1	1	1	.	.
KC		t	Sedum sexangulare	.	33	33	33	33	33	33	33	33	33	33	33	33	33	17	17	33	33	33	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KC	V	t	Veronica verna	.	17	.	.	33	33	17	17	17	17	17	17	17	17	17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KC		t	Pilosella officinarum	17	17	17	17	17	17	17	17	17	17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KC		t	Vulpia myuros	.	.	17	.	17	17	.	.	.	17	.	.	.	17	17	17	.	.	50	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
KC	V	t	Acinos arvensis	17	.	17	17	17	17	17	17	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KC		t	Erodium cicutarium	50	17	33	33	33	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KC		t	Saxifraga tridactylites	.	17	.	.	.	.	.	17	17	17	17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KC	2	t	Jurinea cyanoides	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	1	1	1	.	.	.	.	.	.	.	.	.
KC		t	Myosotis stricta	.	33	17	.	.	.	.	.	.	.	.	17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KC/FB		t	Centaurea stoebe s.l.	50	50	50	50	50	50	67	83	83	83	67	83	100	83	83	83	67	67	67	.	.	.	1	1	1	1	1	1	3	3	3	3	3	3	3
KC/FB	V	t	Potentilla neumanniana	.	17	.	.	.	17	17	17	17	17	17	17	17	17	17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KC/FB	2	t	Orobanche arenaria	.	.	.	.	.	.	.	.	.	.	.	17	17	.	17	17	17	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.
FB		t	Artemisia campestris	67	67	67	83	83	83	100	100	100	100	100	100	100	100	100	100	100	100	100	.	1	3	3	3	3	3	3	3	3	3	3	3	3	3	3
FB	2	t	Fumana procumbens	.	33	33	50	67	67	67	67	67	67	67	67	67	67	67	67	67	67	50	.	.	1	1	1	1	1	1	1	1	1	1	1	1	1	1
FB	3	t	Euphorbia seguieriana	.	.	67	83	83	83	83	100	100	100	100	100	100	100	100	100	100	100	100	.	2	3	3	3	3	3	3	3	3	3	3	3	3	3	3
FB		t	Euphorbia cyparissias	67	50	50	50	67	67	67	67	67	67	50	50	50	50	33	33	17	17	.	.	.	.	1	1	1	1	1	1	1	1	1	1	1	1	1
FB	V	t	Asperula cynanchica	17	50	67	67	67	67	67	67	67	67	67	67	67	67	67	67	67	67	67	.	1	1	1	1	1	1	1	1	1	.	.	.	.	.	.
FB		t	Ononis repens subsp. procurrens	.	.	17	17	17	33	33	33	33	33	33	33	33	33	33	33	33	33	33	.	.	.	.	.	.	1	1	1	1	1	1	1	1	1	1
FB	V	t	Dianthus carthusianorum	.	17	17	17	17	17	17	17	17	17	17	33	33	33	33	50	50	50	33	.	.	1	.	.	.	.	.	1	1	1	1	1	1	.	.
FB	V	t	Phleum phleoides	.	.	50	50	83	83	100	100	100	100	100	100	100	100	100	67	67	83	83	.	.	.	.	.	.	.	.	.	.	2	2	1	2	2	2
FB	V	t	Hippocrepis comosa	.	17	50	33	67	67	50	33	33	50	50	50	50	50	17	.	17	17	17	.	.	.	.	.	.	.	1	.	.	.	1	1	1	.	.
FB	3	t	Stipa capillata	.	17	17	33	33	17	17	17	17	17	17	.	17	.	.	.	.	.	.	.	.	1	1	1	1	1	1	1	1	.	.	.	.	.	.
FB	V	t	Helianthemum nummularium subsp. obscurum	.	33	67	67	83	83	83	67	83	83	83	83	100	100	100	100	50	33	33	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
FB	3	t	Koeleria macrantha	.	.	.	17	17	17	17	17	17	17	17	17	17	17	17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
FB		t	Galium verum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	17	17	17	.	.	.	.	.	.	.	.	.	1	1	1	1	1	.	.
FB	3	t	Allium sphaerocephalon	.	.	.	.	.	.	.	.	.	.	.	17	.	.	.	17	33	.	50	.	.	.	.	.	.	1	.	.	.	.	.	1	.	.	1
FB		t	Ranunculus bulbosus	.	17	17	17	17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
FB		t	Medicago lupulina	67	17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
St			Bromus tectorum	17	50	83	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	.	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3
St			Erigeron canadensis	17	100	100	100	50	33	50	50	50	50	33	33	.	.	.	.	.	.	.	.	1	2	3	3	3	3	3	3	3	2	1	.	2	2	.
St			Papaver dubium	.	.	33	.	17	17	.	.	.	.	.	.	.	.	.	.	.	17	33	.	3	2	.	.	.	.	.	1	1	1	.	1	1	1	1
St			Bromus sterilis	50	67	33	33	50	33	17	.	.	.	.	.	.	.	.	.	.	.	33	.	.	2	1	.	.	.	.	.	.	.	.	1	.	1	1
St			Salsola tragus	83	100	83	67	100	17	17	.	.	.	.	.	.	.	.	.	.	.	.	.	2	2	2	2	2	1	.	.	.	.	.	.	.	.	.
St			Veronica arvensis	.	50	50	50	50	.	.	.	.	.	.	33	33	33	33	33	33	50	50	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
St			Setaria viridis	83	.	.	.	.	.	.	17	33	33	.	.	.	.	.	.	50	.	.	.	1	.	.	1	.	.	1	.	.	.	.	.	1	.	.
St			Fallopia convolvulus	50	33	33	17	50	17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	1	.	.	.	.	.	.	.	.	.	.	.	.	.
St			Vicia hirsuta	.	.	.	.	17	17	17	.	.	.	.	.	.	17	17	.	.	17	17	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.
St			Plantago arenaria	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	1	.	1	1	1	1	1	.	.	.	.	.	.
St			Apera spica-venti	.	67	83	50	33	67	.	.	.	17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.
St			Bromus hordeaceus subsp. hordeaceus	.	67	33	.	17	.	.	.	.	.	.	.	.	.	.	.	.	.	17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1
St			Chenopodium album	83	67	33	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.
St			Papaver rhoeas	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	1	1	1	.	.	.
St			Amaranthus blitoides	50	.	.	17	17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
St			Digitaria sanguinalis s.l.	100	.	17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
St			Viola arvensis s.l.	17	33	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
St			Sisymbrium altissimum	33	.	17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
St			Eragrostis minor	50	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
St			Senecio vernalis	.	50	17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
St			Senecio vulgaris	.	17	17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
St			Lactuca serriola	.	67	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.
St			Polygonum aviculare agg.	100	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
St			Amaranthus retroflexus	67	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
St			Chenopodium striatiforme	67	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
St			Echinochloa crus-galli	33	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
St			Solanum nigrum	17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
St			Veronica persica	17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
St			Arabidopsis thaliana	.	17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ag			Cynodon dactylon	.	.	17	17	50	50	50	50	50	50	50	50	50	50	50	50	50	50	17	.	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
AgR			Calamagrostis epigejos	.	17	33	50	67	67	67	100	100	83	83	83	83	50	50	50	50	17	17	.	.	2	2	2	2	2	2	2	2	2	2	2	2	1	.
Ag			Elymus repens s.l.	83	83	100	100	100	100	100	100	100	83	50	50	50	50	33	.	.	.	.	.	2	3	3	3	3	3	3	3	3	3	3	1	1	1	.
Ag			Equisetum arvense	.	.	17	17	17	17	17	17	17	17	.	.	.	.	.	.	.	.	.	.	1	2	2	1	2	2	2	1	1	1	1	.	.	.	.
Ag			Poa angustifolia	.	33	33	50	50	50	50	50	50	50	67	67	67	67	67	67	17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ag			Carex hirta	17	17	17	17	17	17	17	17	17	17	17	17	17	17	17	17	17	17	17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ag			Diplotaxis tenuifolia	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ar			Oenothera biennis s.l.	33	50	50	100	100	100	100	100	100	100	100	100	67	67	67	.	.	33	.	.	2	3	3	3	3	3	3	3	2	2	3	2	2	2	1
Ar			Rubus caesius	83	83	67	50	50	50	67	50	67	67	50	50	67	33	17	17	17	17	17	.	.	.	1	1	1	1	.	.	.	.	.	.	.	.	.
Ar			Verbascum densiflorum	.	.	17	.	33	33	17	17	17	17	17	17	17	17	.	17	.	17	.	.	.	.	.	.	.	.	.	1	1	1	1	1	.	.	.
Ar			Berteroa incana	.	.	.	.	17	17	17	17	17	17	17	17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ar			Silene latifolia subsp. alba	17	33	17	17	33	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ar			Rubus fruticosus agg.	.	.	.	17	.	17	17	17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ar			Tragopogon dubius	.	.	.	17	.	.	.	.	.	.	.	.	.	.	.	.	.	17	17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ar			Bryonia dioica	17	17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ar			Urtica dioica	17	17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ar			Daucus carota	.	17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.
Ar			Artemisia vulgaris s.l.	.	.	.	17	17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ar			Galium aparine	.	17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
MA			Dactylis glomerata s.str.	17	50	33	67	67	67	33	50	50	50	33	17	17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
MA			Cerastium holosteoides	.	.	.	.	.	.	.	33	33	33	33	33	33	33	33	33	33	33	33	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
MA			Achillea millefolium agg.	33	33	33	17	17	17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.
MA			Galium album	.	.	17	33	17	17	17	17	17	17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
MA			Plantago lanceolata	17	17	33	.	.	17	17	.	.	.	.	.	.	17	17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
MA			Arrhenatherum elatius	33	2	33	17	17	17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
MA			Lolium perenne	17	50	17	17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
MA			Crepis capillaris	.	50	50	17	17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
MA			Holcus lanatus	.	17	.	.	17	17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
MA			Poa pratensis	17	17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
MA			Trifolium repens	17	17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
os			Festuca ovina agg.	.	.	50	67	67	67	83	83	83	83	83	83	83	83	83	67	67	83	83	.	.	2	2	2	2	2	2	2	3	3	3	3	3	3	3
os			Vicia villosa	.	17	33	33	33	33	33	.	.	50	33	33	17	50	50	33	33	33	33	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
os			Silene vulgaris subsp. vulgaris	17	17	17	33	33	33	33	33	33	33	33	33	33	33	17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
os			Vicia angustifolia	17	33	.	17	.	17	33	.	17	17	.	.	.	17	17	17	17	17	17	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.
os			Thymus pulegioides subsp. pulegioides	.	.	.	.	.	.	.	.	.	.	17	17	17	.	17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
os			Poa annua	33	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
os			Rhinanthus minor	33	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
os			Securigera varia	.	33	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
os			Agrostis stolonifera	.	33	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
os			Poa sp. juv	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.
ws			Pinus sylvestris juv	100	100	100	83	83	67	83	33	33	33	33	33	33	17	17	.	17	.	.	.	3	.	2	1	1	.	1	1	1	1	1	1	.	1	.
ws			Pinus sylvestris shrub layer	.	.	.	.	.	.	50	.	.	.	.	.	.	.	.	.	17	17	17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
ws			Rosa sp. juv	33	33	33	17	17	17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
ws			Rosa sp. shrub layer	.	.	.	.	.	.	17	17	17	17	17	17	17	17	17	17	17	17	17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
ws			Robinia pseudoacacia juv	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	.	.	.	.	1	1	1	1	1	1	.
ws			Robinia pseudoacacia shrub layer	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	1	.	.	.	.	.	.	.	1
ws			Juglans regia juv	.	.	.	17	17	17	.	.	.	17	.	.	.	.	17	17	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.
ws			Cotoneaster, creeping cultivar	17	17	17	17	17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
ws			Prunus avium juv	17	33	17	17	17	17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
ws			Quercus robur juv	.	.	17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
ws			Cytisus scoparius juv	.	.	.	17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
os		L	Cladonia furcata s.l.	67	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	.	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
os	3	L	Peltigera rufescens	.	17	.	17	50	83	83	83	83	100	100	100	100	100	100	100	100	100	100	.	.	.	.	.	.	.	1	1	1	1	1	1	1	1	1
KC/FB	3	L	Cetraria aculeata	.	.	.	.	.	.	.	17	17	17	17	17	17	17	17	.	.	.	17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
KC/FB		B	Syntrichia ruralis var. ruraliformis	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	.	.	2	2	2	2	2	2	2	3	3	3	3	3	3	3
			cover % average	<1	<1	<1	<1	1	2	2	9	12	16	18	22	32	30	38	41	48	47	49	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
os		B	Hypnum cupressiforme var. lacunosum	67	67	67	67	67	67	67	67	67	67	100	100	100	100	100	100	100	100	100	.	.	.	1	1	1	1	1	1	1	3	3	3	3	3	3
			cover % average	<1	<1	<1	<1	<1	<1	<1	1	2	3	6	9	11	15	18	18	21	23	22	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
os		B	Brachythecium albicans	.	.	.	83	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	.	.	.	.	1	1	1	1	1	1	1	1	1	1	1	2
os		B	acrocarpic mosses, not differentiated	.	.	.	.	50	33	.	17	17	17	17	.	.	.	.	.	.	.	.	.	.	.	.	1	1	1	1	.	.	.	.	.	.	.	.
os	V	B	Racomitrium canescens	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	83	83	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1
os		B	Bryum argenteum/cf. argenteum	.	.	.	.	33	33	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Storm et al.: Restoration of *Koelerion glaucae* vegetation in the Upper Rhine valley (Hesse, Germany): an update on the development of a model site after 19 years. – Tuexenia 44 (2024).

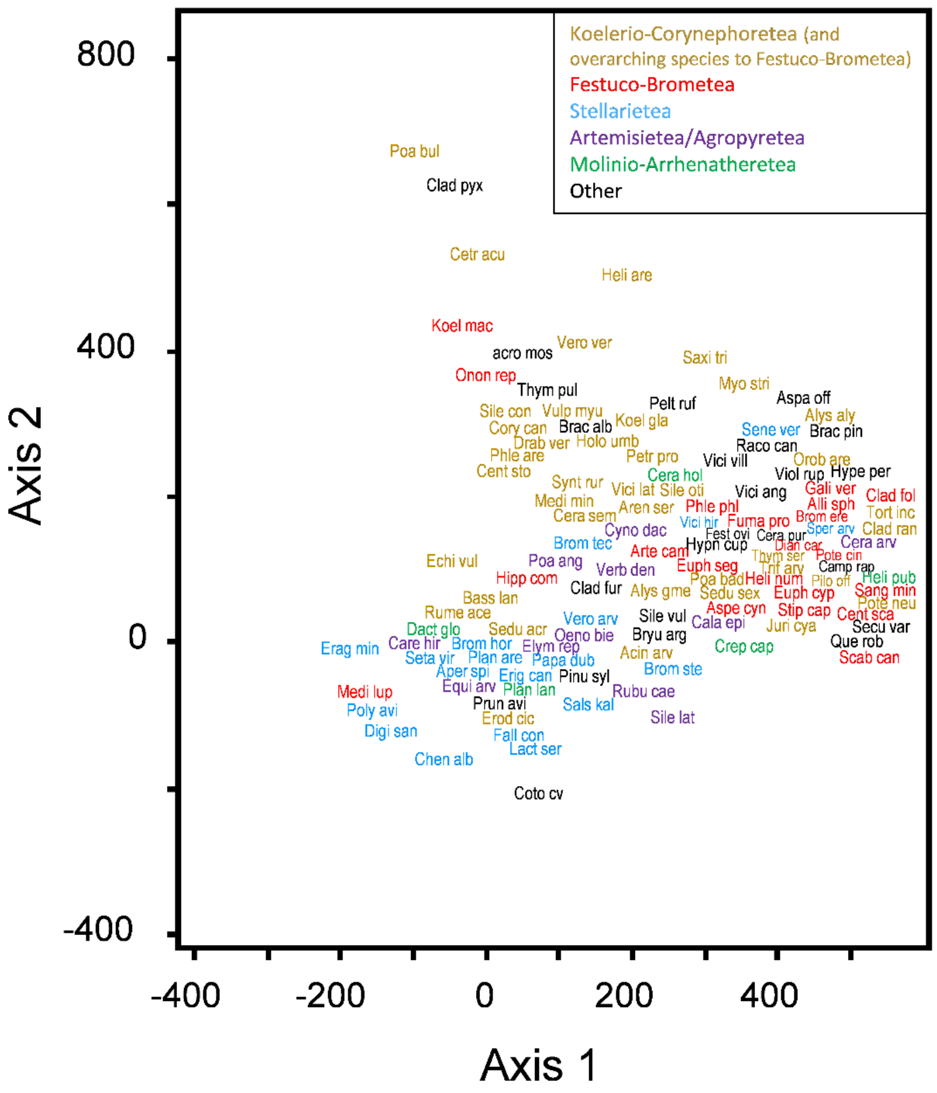
Supplement E1. Detrended correspondence analysis (DCA) as in Fig. 4, based on the rank-transformed Braun-Blanquet data of the large plots (S: small plots). Axis 1 explains 52% and axis 2 another 20% of the variance in the data set.

Anhang E1. Detrended Correspondence Analysis (DCA) wie in Abb. 4 für die rangtransformierten Daten der großen Plots (S: kleine Plots). Achse 1 erklärt 52% und Achse 2 weitere 20% der Varianz des Datensatzes.



Supplement E2a. Detrended correspondence analysis (DCA) as Fig. 4, but with species shown instead of plots. See E2b for species abbreviations. Colors indicate the phytosociological affiliation of the species. 28 species with ≤ 5 occurrences were not displayed for clarity of the diagram (the target species *Potentilla cinerea* subsp. *incana* with four occurrences was retained). Some overlapping species names were separated for better readability.

Anhang E2a. Detrended Correspondence Analysis (DCA) wie in Abb. 4, aber mit Darstellung der Arten anstelle der Plots. Abkürzungen der Arten siehe E2b. Die Farben geben die Zuordnung zu den pflanzensoziologischen Klassen an. 28 Arten mit ≤ 5 Vorkommen wurden zugunsten der Klarheit des Diagramms nicht dargestellt (die Zielart *Potentilla cinerea* subsp. *incana* mit vier Vorkommen wurde beibehalten). Einige überlappende Artnamen wurden für die bessere Lesbarkeit etwas auseinandergezogen.



Supplement E2b. Species abbreviations in E2a. B = bryophytes, L = lichens.

Anhang E2b. Abkürzungen der Arten in E2a. B = Moose, L = Flechten.

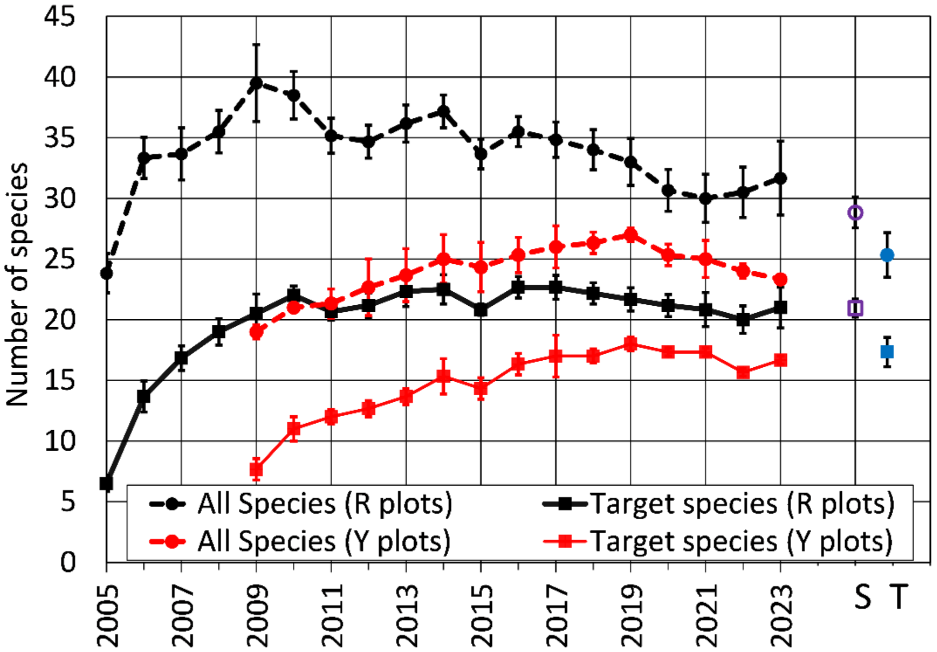
Abbreviation	Species	B/L
Acin arv	Acinos arvensis	
acro mos	acrocarpic mosses	B
Alli sph	Allium sphaerocephalon	
Alys aly	Alyssum alyssoides	
Alys gme	Alyssum gmelinii	
Aper spi	Apera spica-venti	
Aren ser	Arenaria serpyllifolia agg.	
Arte cam	Artemisia campestris	
Aspa off	Asparagus officinalis	
Aspe cyn	Asperula cynanchica	
Bass lan	Bassia laniflora	
Brac alb	Brachythecium albicans	B
Brac pin	Brachypodium pinnatum	
Brom ere	Bromus erectus	
Brom hor	Bromus h. subsp. hordeaceus	
Brom ste	Bromus sterilis	
Brom tec	Bromus tectorum	
Bryu arg	Bryum argenteum/cf. argenteum	B
Cala epi	Calamagrostis epigejos	
Camp rap	Campanula rapunculus	
Care hir	Carex hirta	
Cent sca	Centaurea scabiosa	
Cent sto	Centaurea stoebe s.l.	
Cera arv	Cerastium arvense	
Cera hol	Cerastium holosteoides	
Cera pur	Ceratodon purpureus	B
Cera sem	Cerastium semidecandrum	
Cetr acu	Cetraria aculeata	L
Chen alb	Chenopodium album	
Clad fol	Cladonia foliacea	L
Clad fur	Cladonia furcata s.l.	L
Clad pyx	Cladonia pyxidata agg.	L
Clad ran	Cladonia rangiformis	L
Cory can	Corynephorus canescens	
Coto cv	Cotoneaster cultivar	
Crep cap	Crepis capillaris	
Cyno dac	Cynodon dactylon	
Dact glo	Dactylis glomerata s. str.	
Dian car	Dianthus carthusianorum	
Digi san	Digitaria sanguinalis s.l.	
Drab ver	Draba verna	
Echi vul	Echium vulgare	
Elym rep	Elymus repens s. str.	
Equi arv	Equisetum arvense	
Erag min	Eragrostis minor	
Erig can	Erigeron canadensis	
Erod cic	Erodium cicutarium	
Euph cyp	Euphorbia cyparissias	
Euph seg	Euphorbia seguieriana	
Fall con	Fallopia convolvulus	
Fest ovi	Festuca ovina agg.	
Fuma pro	Fumana procumbens	
Gali ver	Galium verum	
Heli are	Helichrysum arenarium	
Heli num	Helianthemum nummularium subsp. obscurum	
Heli pub	Helictotrichon pubescens	
Hipp com	Hippocrepis comosa	
Holo umb	Holosteum umbellatum	
Hype per	Hypericum perforatum	

Abbreviation	Species	B/L
Hypn cup	Hypnum cupressiforme var. lacunosum	B
Juri cya	Jurinea cyanoides	
Koel gla	Koeleria glauca	
Koel mac	Koeleria macrantha	
Lact ser	Lactuca serriola	
Medi lup	Medicago lupulina	
Medi min	Medicago minima	
Myo stri	Myosotis stricta	
Oeno bie	Oenothera biennis s.l.	
Onon rep	Ononis repens subsp. procurrens	
Orob are	Orobanche arenaria	
Papa dub	Papaver dubium	
Pelt ruf	Peltigera rufescens	L
Petr pro	Petrorhagia prolifera	
Phle are	Phleum arenarium	
Phle phl	Phleum phleoides	
Pilo off	Pilosella officinarum	
Pinu syl	Pinus sylvestris juv + shrub	
Plan are	Plantago arenaria	
Plan lan	Plantago lanceolata	
Poa ang	Poa angustifolia	
Poa bad	Poa badensis	
Poly avi	Polygonum aviculare agg.	
Pote cin	Potentilla cinerea subsp. incana	
Pote neu	Potentilla neumanniana	
Prun avi	Prunus avium juv	
Que rob	Quercus robur juv	
Raco can	Racomitrium canescens	
Rubu cae	Rubus caesius	
Rume ace	Rumex acetosella	
Sals kal	Salsola tragus	
Sang min	Sanguisorba minor	
Saxi tri	Saxifraga tridactylites	
Scab can	Scabiosa canescens	
Secu var	Securigera varia	
Sedu acr	Sedum acre	
Sedu sex	Sedum sexangulare	
Sene ver	Senecio vernalis	
Seta vir	Setaria viridis	
Sile con	Silene conica	
Sile lat	Silene latifolia subsp. alba	
Sile oti	Silene otites	
Sile vul	Silene v. subsp. vulgaris	
Sper arv	Spergula arvensis	
Stip cap	Stipa capillata	
Synt rur	Syntrichia ruralis var. ruraliformis	B
Thym pul	Thymus pulegioides subsp. pulegioides	
Thym ser	Thymus serpyllum	
Tort inc	Tortella inclinata	B
Trif arv	Trifolium arvense	
Verb den	Verbascum densiflorum	
Vero arv	Veronica arvensis	
Vero ver	Veronica verna	
Vici ang	Vicia angustifolia	
Vici hir	Vicia hirsuta	
Vici lat	Vicia lathyroides	
Vici vill	Vicia villosa	
Viol rup	Viola rupestris	
Vulp myu	Vulpia myuros	

Storm et al.: Restoration of *Koelerion glaucae* vegetation in the Upper Rhine valley (Hesse, Germany): an update on the development of a model site after 19 years. – Tuexenia 44 (2024).

Supplement E3. Mean number of target species in comparison to all species of the large restoration plots (black: R, red: Y) over the course of the study period. The plots at the reference sites are depicted in purple (S: small plots) or blue (T) on the right side of the diagram. Solid lines and quadrats: target species, dashed lines and round symbols: all species. Error bars indicate the standard errors of the six (R) or three plots (Y, S, T).

Anhang E3. Mittlere Zielartenzahlen im Vergleich zu den Gesamtartenzahlen der großen Restitutions-Plots (schwarz: R, rot: Y) im Verlauf der Untersuchungsperiode. Die Plots der Referenzflächen sind in violett (S: kleine Plots) bzw. blau (T) rechts im Diagramm eingetragen. Durchgezogene Linien und Quadrate: Zielartenzahl, gestrichelte Linien und runde Symbole: Gesamtartenzahl. Die Fehlerbalken geben die Standardfehler der sechs (R) bzw. drei Plots (Y, S, T) an.



Storm et al.: Restoration of *Koelerion glaucae* vegetation in the Upper Rhine valley (Hesse, Germany): an update on the development of a model site after 19 years. – Tuexenia 44 (2024).

Supplement E4. Mean target species ratios (TSR) of the large restoration plots (filled symbols; black: R, red: Y) in comparison to the small plots (open symbols; olive: R, green: Y) over the course of the study period. The plots at the reference sites are depicted in purple (S) or blue (T) on the right side of the diagram. Solid lines and round symbols: TSR_{qual}, dashed lines and quadrats: TSR_{quant}. No error bars of the six (R) or three plots (Y, S, T) are indicated for the clarity of the diagram (see for error bars, Fig. 12).

Anhang E4. Mittlere Zielarten-Ratios (TSR) der großen Restitutions-Plots (ausgefüllte Symbole; schwarz: R, rot: Y) im Vergleich zu den kleinen Plots (offene Symbole; oliv: R, grün: Y) im Verlauf der Untersuchungsperiode. Die Plots der Referenzflächen sind in violett (S) bzw. blau (T) rechts im Diagramm eingetragen. Durchgezogene Linien und runde Symbole: TSR_{qual}, gestrichelte Linien und quadratische Symbole: TSR_{quant}. Es sind keine Fehlerbalken der sechs (R) bzw. drei Plots (Y, S, T) angegeben, damit das Diagramm übersichtlich bleibt (s. zu den Fehlerbalken auch Abb. 12).