



RESEARCH ARTICLE

Grassland restoration practice in Central Europe: drivers of success across a broad moisture gradient

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Ongoing ecosystem degradation and loss demand restoration efforts worldwide. In Central Europe, semi-natural grasslands are in focus, and better understanding of restoration success and its drivers is needed. For practical projects, systematic screening remains lacking. We compared plant species composition of 41 recipient sites 3–18 years after restoration via plant material transfer with composition of their donor sites. Further, we analyzed establishment of habitat-typical and endangered species. Spanning a gradient of moisture conditions, sites were located in Germany and Luxembourg. Soil characteristics, biomass productivity, and restoration setup (e.g. previous site state, age) were investigated as potential drivers of success. In dry grasslands, success was highest, likely due to the creation of raw soils at several sites before plant material application. While raw soils generally favored the establishment of endangered species, the resulting low-productive and dry conditions sometimes posed challenges for mesic grassland restoration. In mesic grasslands, elevated soil pH of some recipient sites further contributed to divergence in species composition compared to donor sites. In alluvial grasslands, high nutrient and productivity levels of recipient sites impeded restoration success. Wet grasslands were successfully restored when soil moisture was sufficient. Across grassland types, species richness decreased with time since restoration, yet the number and cover of habitat-typical and endangered species remained stable. Introducing typical species in addition to plant material transfer supported restoration. We advocate for large-scale, systematic investigations of practical grassland restoration projects combined with well-defined monitoring guidelines across different regions to address this complex challenge in the coming decades.

Key words: abiotic conditions, green hay transfer, monitoring, plant material transfer, raw soil, Red List species, species composition, success factors

Implications for Practice

- Recipient and donor sites for grassland restoration using plant material transfer should be chosen with strong focus on abiotic matching, ideally supported by soil analyses. Raw soils should only be created on the recipient sites when restoring low-productive grassland types, such as dry grasslands.
- Ensuring sufficiently low nutrient levels and productivity as well as an adequate moisture regime is crucial for successful restoration of alluvial and wet grasslands.
- Restoration measures and site locations should be thoroughly documented to enable accurate assessment of success, including vegetation development. When restoration is conducted on existing grasslands, the species pool should be recorded prior to implementation.

Introduction

Landscapes in Europe and worldwide are under increasing pressure from rapid climate change. Ecosystem services such as resilient biomass and food production (Munsch et al. 2022), biodiversity support (Habibullah et al. 2022), and esthetic and cultural value (Aktürk & Dastgerdi 2021) are under severe threat (Scholes 2016). While healthy and species-rich ecosystems are crucial for buffering climate impacts on service provision (Härdtle 2024), land

use changes have often resulted in systems highly vulnerable to these stressors (Munsch et al. 2022). To tackle these challenges, large-scale restoration of degraded ecosystems is urgently required. The urgency is underscored by global initiatives such as the UN Decade on Ecosystem Restoration (UN General Assembly 2019) and legislative measures such as the Nature Restoration Law of the European Union (Regulation [EU] 2024/1991).

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In practice, successful restoration relies on thorough understanding and careful consideration of relevant success factors. Scientific evidence highlights that, particularly on social and organizational levels, certain universally important factors are identifiable across various ecosystem types. These include trustful collaboration among the involved persons or institutions, a sense of community with and among local stakeholders, and growing restoration experience with time. These factors were found to enhance restoration success in systems such as riverine habitats (Gamborg et al. 2019), mangrove forests (Lhosupasirirat et al. 2023), and semi-natural grasslands (Sommer et al. 2023b). The critical role of suitable abiotic conditions in supporting the target ecosystems is also well known (Hallett et al. 2013). However, successful restoration must also address specific challenges and implement targeted measures reflecting regional particularities and ecosystem-specific needs. In Europe, semi-natural grasslands are of particular concern (Waldén & Lindborg 2018; Schneider et al. 2023), as they are shaped by a long land use history with pronounced regional differences (Kapfer 2010).

Mowing a species-rich semi-natural grassland site enables simultaneous collection of seeds from a diverse range of typical plant species with the harvested plant material. This approach can facilitate grassland restoration. Seed-containing plant material collected from a donor site can be transferred to a target site of restoration (i.e. the “recipient site”), serving as the foundation for establishing a target plant community (Kiehl et al. 2010). Species transfer is not limited to vascular plants but can also include cryptogams (Michalska-Hejduk et al. 2017) and invertebrates (Stöckli et al. 2021). Restoration success is supported by careful selection of appropriate species-rich donor sites (Török et al. 2011; Wagner et al. 2021), by using multiple donor sites (Dittberner et al. 2019), and by additionally introducing species absent from the donor sites or lacking ripe seeds at the time of collection (Hofmann et al. 2020). Still, productivity and abiotic conditions of recipient sites are critical factors for restoration success (Török et al. 2011; Sommer et al. 2023a). However, these conditions should not be considered in isolation but must generally align with those of the donor sites to support establishment and persistence of transferred plant populations (Scotton et al. 2012; De Vitis et al. 2022).

Scientific knowledge on the effectiveness and key success factors of grassland restoration with plant material transfer has often been derived from targeted experimental settings designed to address specific research questions (e.g. Eckstein & Donath 2005; Hansen et al. 2022; Sommer et al. 2023a). Restoration measures planned and conducted in practice, where the primary focus is on achieving restoration goals rather than answering research questions, are often monitored for their effectiveness as well. However, systematic and standardized evaluations across many of such projects are rare, though they may enable identification of success factors particularly relevant in practice (Biro et al. 2024). Practitioner interviews conducted in a previous study revealed a mixed picture of success and highlighted different drivers of restoration success depending on the grassland type (Sommer et al. 2023b).

In this study, we aimed to quantify restoration success across a diverse panel of practical plant material transfer projects and to

explore drivers of success or failure. Our dataset spanned a considerable gradient in soil moisture covering dry, mesic, alluvial, and wet grasslands, defining four different target habitat types of restoration. Specifically, we addressed the following research questions:

- (a) Which success levels were achieved in the restoration of different grassland types?
- (b) Which factors drove restoration success within the different grassland types?
- (c) Which factors affected restoration success across all grassland types?

Methods

Study Regions and Restoration Measures

The restoration projects investigated in this study are located in Luxembourg and the German federal states of Brandenburg, Hesse, North Rhine-Westphalia, Rhineland-Palatinate, and Saarland. We acquired the sites from partners of an interview study (Sommer et al. 2023b), aiming at a broad spectrum of grassland types covering a moisture gradient. Most projects were practical projects not guided by scientific questions. To enlarge the dry grassland panel, we included three recipient sites from science-practice cooperations: Sites 4 (Storm et al. 2022), 5, and 6 (both from Storm et al. 2016; see Table S1 for details on recipient sites). Mean annual temperature in the study regions ranges from 5.9 to 11.4°C and mean annual precipitation from 510 to 1289 mm (Deutscher Wetterdienst 2023; means from 1991 to 2020 for the closest weather stations, respectively). Elevation ranges from 23 to 778 m a.s.l.

From the project partners, we collected detailed information on site characteristics and the restoration process (see Table S1). In total, we investigated 37 donor sites (size of 0.07–6.82 ha) and 41 recipient sites (0.02–11.9 ha) of plant material transfer. Individual donor sites were used to transfer plant material to one to four recipient sites, and material from one to four donor sites was applied to individual recipient sites. The measures had been carried out 3–18 years before our investigation. We categorized the recipient sites based on the respective donor sites, defining four target grassland types, that is, *dry* grasslands, *mesic* grasslands, *alluvial* grasslands with alternating water conditions, and *wet* grasslands (Section 4).

Before restoration, most recipient sites had been grasslands, arable fields (with crop production abandoned up to one season before restoration), or spruce plantations (Table S1; see proportions in Fig. 1). Extant vegetation was reduced by combinations of mowing, mulching (cutting without removal of the clippings), or clearing, and soil preparation measures (plowing, rotovating, and forestry mulching). Some recipient sites were newly created by depositing humus-containing topsoil or humus-free sand, with the latter resulting in raw soil surfaces. On several sites, raw soils were created by topsoil removal or excavation to reduce competition with extant vegetation and plants emerging from the soil diaspore bank. In most cases, the transferred plant material was freshly cut; sometimes, the material was cut and dried or raked without prior cutting. On several recipient sites, additional plant species were introduced by sowing or planting

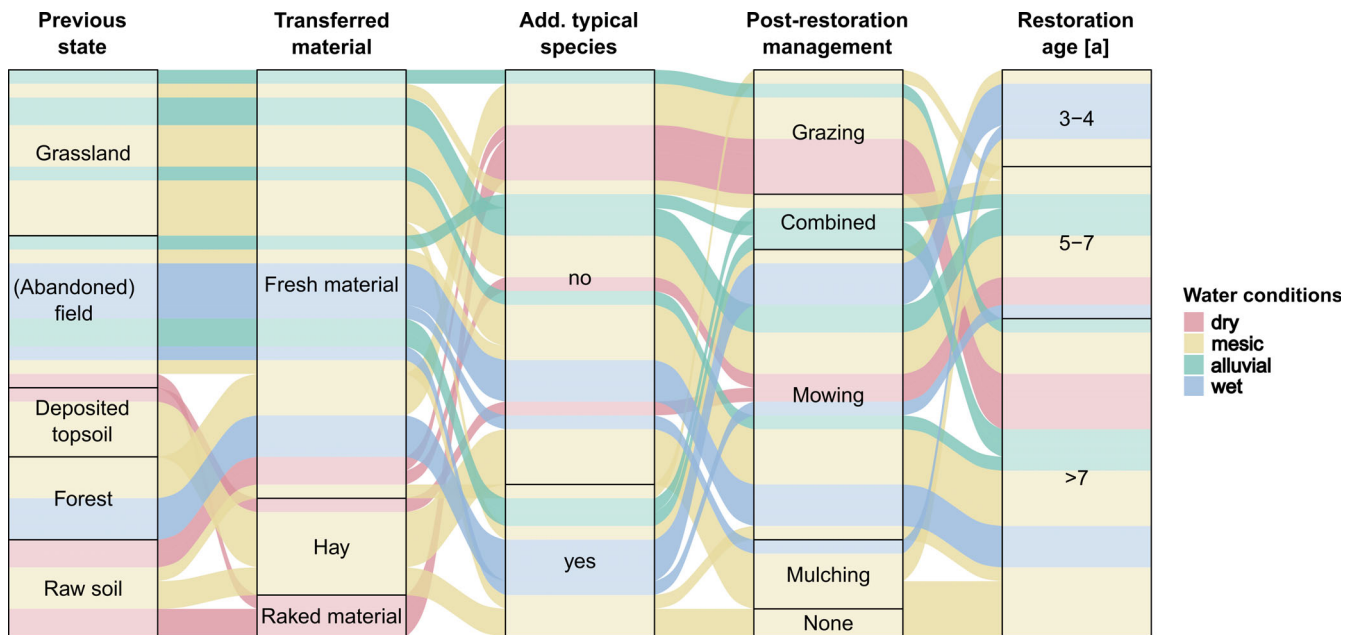


Figure 1. Setup of the restoration process for the 41 recipient sites, grouped by the target grassland types as defined by the donor sites (*dry* grasslands, *mesic* grasslands, *alluvial* grasslands with alternating water conditions, and *wet* grasslands). The width of each strip represents the proportion of recipient sites with the respective combination of previous land use or state, the type of transferred plant material, additional introduction of typical plant species, post-restoration management, and restoration age in years.

using different methods. After plant material transfer, most sites were low-intensively managed. This was done by grazing, mowing, a combination of both, or mulching.

Vegetation, Biomass, and Soil Sampling

Between 9 May and 4 July 2022, prior to the respective first cut or grazing, we visited all recipient and donor sites. Depending on the size of the sites, we placed two (<0.2 ha), three (0.2–2 ha), or four (>2 ha) 25 m² plots. In total, 118 plots were located on 37 donor sites and 110 plots on 41 recipient sites of restoration. We recorded all vascular plant species using the Braun-Blanquet scale modified by Reichelt and Wilmanns (1973). Nomenclature followed the German species list (Jansen & Dengler 2008), version 1.5, and data were organized in TURBOVEG (Hennekens & Schaminée 2001). For data analysis, the Braun-Blanquet scale was transformed to cover percentages following Schmiede et al. (2012).

As structural habitat characteristics, we estimated the cover of vascular plants, litter, mosses, lichens, and the share of open soil or bare rock, and measured the average height of the upper herb layer. Aboveground biomass was cut from four 0.1 m² squares per plot and merged into one mixed sample. For each plot, we collected composite samples of four topsoil cores (0–10 cm), using a soil corer of 2.5 cm diameter. For comparability, we sampled corresponding donor and recipient sites within ≤10 days. Deviations from this procedure are listed in Supplement S1. The comparative plot-based vegetation data of corresponding recipient and donor sites are documented in Table S2.

Biomass and Soil Analyses

After drying at 60°C for 48 hours, biomass samples were weighed, and dry matter yield was calculated as a productivity measure. Then, the biomass samples were milled to 0.5 mm, and nitrogen (N), potassium (K), and phosphorus (P) concentrations were determined via near infrared spectroscopy (SpectraStar 2600XTR, Unity Scientific, Columbia, MD, U.S.A.). For methodological details, see Kleinebecker et al. (2011). Biomass nutrient concentrations were used to calculate N/P and N/K ratios. Soil samples were air-dried and sieved to 2 mm. Soil pH was measured in CaCl₂ solution. Extraction with calcium-acetate-lactate solution (CAL) was performed to determine plant-available K and P (Blume et al. 2000). Total soil N and carbon (C) concentrations were determined using a C-N-S element analyzer (Unicube, Elementar, Germany). The organic C content was calculated as the difference between total C and inorganic C, which was determined with the Scheibler method (Blume et al. 2000), and the C/N ratio was calculated as the ratio between organic C and total N content.

Definition of Target Grassland Types

We grouped the 41 recipient sites based on their corresponding donor sites into four major target grassland types of restoration. First, we defined three moisture categories (dry, mid-level, and wet) by k-means clustering of the unweighted mean Ellenberg moisture (*F*) values (Ellenberg et al. 2001; Klotz et al. 2002) of the species recorded in the corresponding donor sites. The donor sites of the mid-level category comprised mesic grasslands and alluvial grasslands characterized by species indicating

alternating water conditions. Thus, we performed a second k-means clustering separating the mid-level category into two groups based on the proportion of Ellenberg indicator species for alternating moisture conditions. The resulting four target grassland types of restoration are listed below, with the main plant alliances (Mucina et al. 2016) of the respective donor sites, the corresponding habitat types (European habitats directive; BfN 2018 and, for *Calthion palustris*, Luxembourg classification; MECDD 2023), and the number of assigned recipient sites in parentheses:

- Dry grasslands on sandy and rocky substrates (alliances—*Festucion valesiacae*, *Koelerion glaucae*, *Xerobromion erecti*, *Bromion erecti*; habitat types—6120, 6210; six sites).
- Mesic grasslands of differing acidity and altitude (*Arrhenatherion elatioris*, *Phyteumato-Trisetion*, *Nardion strictae*; 6510, 6520, 6230; 20 sites).
- Alluvial grasslands with alternating moisture conditions (*Molinion caeruleae*, *Cnidion dubii*; 6410, 6440; seven sites).
- Wet grasslands (*Molinion caeruleae*, *Calthion palustris*; 6410, BK10; eight sites).

Assessment of Restoration Success

As a variable of restoration success and implying that practitioners chose donor sites of high conservation value, we calculated for each recipient site plot the

- (a) compositional similarity to the corresponding donor site(s).

The compositional similarity was defined as the Bray–Curtis similarity of the vegetation composition (cover percentages) of a recipient site plot and the corresponding donor site plots, which were pooled by averaging the cover percentages of each recorded species.

As additional variables of restoration success, we used the

- (b) species number per 25 m²,
- (c) number of typical species per 25 m²,
- (d) cover of typical species,
- (e) number of Red List species per 25 m², and
- (f) cover of Red List species.

Species were considered typical of a grassland type (dry/mesic/alluvial/wet) if they were characteristic of at least one of the corresponding main habitat types (6120, 6210/6510, 6520, 6230/6410, 6440/6410, BK10) according to BfN (2018) and MECDD (2023). Red List species were defined as such if their status in the Red List of Germany (Metzing et al. 2018) was V (“near threatened”), 3 (“vulnerable”), 2 (“endangered”), or 1 (“critically endangered”).

Furthermore, as species-based indicators for the degree of human influence on habitats (Erdős et al. 2022), we investigated naturalness and hemeroby (Supplement S2).

Analysis of Species Composition

All statistical analyses were performed using R version 4.4.1 (R Core Team 2023). To explore deviations in vegetation

composition between donor and recipient sites and underlying environmental gradients, we performed ordination analyses on the plot-based vegetation data separately for each target grassland type. Based on species cover and the Bray–Curtis dissimilarity, we applied non-metric multidimensional scaling (NMDS; function “metaMDS” of the “vegan” package—Oksanen et al. 2020), with a first run of max. one hundred random start configurations. The second run was performed analogously but used the lowest-stress solution from the first run as the starting configuration. We opted for two-dimensional solutions for all target grassland types after visually checking the decrease of stress with increasing number of dimensions (Leyer & Wesche 2008). Using the “envfit”-function, we fitted vectors for the variables of habitat structure, biomass and soil characteristics, community characteristics (unweighted mean Ellenberg indicator values, proportions of changing moisture (symbol “~”) or wetness (“=”) indicators, proportions of different life span groups in the species pool of a plot, based on Klotz et al. 2002), and the different variables of restoration success. We further visualized restoration age, introduction of additional typical species, and previous state of the recipient sites.

Identification of Success Factors Across Grassland Types

To identify factors determining restoration success across target grassland types, we used generalized linear (mixed) models (GL [M]Ms) on the plot level (Table 1). For analyses on naturalness and hemeroby, see Supplement S2. We chose model types by visually checking the best-fitting response distributions (R package “fitdistrplus,” Delignette-Muller et al. 2023). For modeling, we used the glm function if possible and used the “glmmTMB” package (Brooks et al. 2024) for beta-distributed response variables. For the cover of Red List species, we applied a zero-inflated model with an observation-level random effect included to avoid overdispersion and used the optimizer “optim” to overcome convergence problems. In all models, the target grassland type was included as a fixed effect.

Using the “dredge” function (package MuMIn, Barton 2020), we selected explanatory variables for the final models from the following set of variables (see correlations in Fig. S1): soil C/N ratio, organic C, plant-available P and K, pH value, dry matter yield, N/P and N/K ratio in the biomass, restoration age, use of multiple donor sites (yes/no), raw soil as previous state (yes/no), and introduction of additional species (yes/no). For the success variables referring to Red List or typical species, only the additional introduction of such species was considered. The models with the lowest Akaike information criterion (AIC) containing a maximum of five explanatory variables were selected as final models. The final models were visually checked for normality of residuals and homogeneity of variances across the ranges of the response estimates and predictors (DHARMA package, Hartig & Lohse 2022). Furthermore, we checked the variance inflation factors (VIF), which were always less than 5, indicating no multicollinearity issues. For the generalized models (Poisson or beta distribution), the squared correlation between the response and the predicted values was calculated as a measure of R^2 .

Recipient site plots of mesic grasslands made up almost half of the observations (51 out of 105). In addition, the NMDS for

Table 1. Overview of the (generalized) linear (mixed) models selected for the variables of restoration success. In the first two rows, the assumed response distribution and the R package used for modeling are given. Below, the model intercept and, for the cover of Red List species, the intercept of the applied zero-inflation (ZI) model are presented. These are followed by the estimates of the effects of the different target grassland types and of the explanatory variables considered for model selection (significance levels: *** $p \leq 0.001$, ** $p \leq 0.01$, * $p \leq 0.05$; no entry—not selected; n.c.—not considered for selection). The effect directions of the Boolean variables (y/n—yes/no) refer to the “yes” state. In the bottom part of the table, the variance explained by the observation-level random effect (only included for the cover of Red List species) is given, along with the number of observations and the r^2 of the models.

	Similarity to donor site(s)	Species number	Number of typical species	Cover of typical species	Number of Red List species	Cover of Red List species
Distribution	Beta	Normal	Normal	Normal	Poisson	Beta
Package	glmmTMB	stats	stats	stats	stats	glmmTMB
Intercept	1.488*	43.931***	24.040***	1.007***	1.280***	−3.466***
Intercept (ZI model)						−1.061***
Mesic target (y/n)	−0.740***	−2.824	3.251	0.123	−1.744***	−1.594***
Alluvial target (y/n)	−1.230***	−2.013	−15.457***	−0.331***	−1.112***	−0.757
Wet target (y/n)	−0.824***	6.742*	−5.815**	−0.391***	−0.537*	0.151
Soil C/N ratio	−0.036					
Soil organic C (%)						−0.094*
Soil K (mg/100 g)		0.362*	0.513***	0.010*	0.041***	0.064**
Soil P (mg/100 g)		−0.404*	−0.242*			0.068*
Soil pH	−0.175***	−1.505*	−1.665***	−0.111***		
Dry matter yield (g/m ²)	0.001			0.001***		
N/K ratio in biomass						
N/P ratio in biomass						
Multiple donor sites (y/n)	−0.249	3.131	−3.543*	−0.090	−0.439*	−1.133***
Raw soil (y/n)					0.717***	1.123**
Add. species (y/n)			n.c.	n.c.	n.c.	n.c.
Add. typical species (y/n)	n.c.	n.c.	3.554**		n.c.	n.c.
Add. Red List species (y/n)	n.c.	n.c.	n.c.	n.c.		
Restoration age (a)	−0.029*	−0.696***		−0.009		
Observation variance						0.953
Number of observations	105	105	105	105	105	105
R^2	0.304	0.417	0.694	0.680	0.680	0.985

mesic grasslands (Fig. 4B) did not show associations of restoration success variables with environmental gradients or species characteristics. To support our interpretation of the model selection output across grassland types and our identification of restoration success factors in mesic grasslands, we performed an analogous model selection only for the latter (Table S3, Supplement S2). Accordingly, no fixed effect for the target grassland type of restoration was included. Out of the explanatory variables, soil C/N ratio and soil organic C were strongly correlated ($r = 0.77$), which led to multicollinearity ($VIF \geq 5$) in the five lowest-AIC models for the number of Red List species. Thus, the sixth model in the selection list of the “dredge” function was chosen as the final model for this variable.

Results

Restoration Success

The compositional similarity of the recipient sites and corresponding donor sites varied strongly within all four grassland types (Fig. 2A). Alluvial grasslands usually had a lower similarity between recipient sites and donor sites (mean of 0.22) compared to the other grassland types (mean of 0.33). Species numbers were similar across grassland types and between donor and recipient sites within the grassland types (overall mean 29.6 species per 25 m²; Fig. 2B). Only in wet grasslands were

recipient sites markedly more species-rich than donor sites (mean of 40.0 vs. 28.9 per 25 m²). There was a general trend toward lower numbers and cover of typical and Red List species in the recipient sites compared to the donor sites across grassland types (Fig. 2C–F). However, this was not completely consistent. The cover of typical species was similar in donor and recipient sites in mesic (combined mean of 74.2%) and alluvial grasslands (22.8%). In dry grasslands, the same held true for the number of Red List species (combined mean of 5.5 per 25 m²) as well as their cover (10.3%). In contrast, in alluvial grasslands, the number and cover of Red List species were pronouncedly higher in donor sites compared to recipient sites (mean number: 7.0 vs. 1.9 per 25 m², mean cover: 11.6 vs. 3.3%). Concerning naturalness, the patterns between grassland types and donor and recipient sites largely followed those observed for typical and Red List species (Fig. S2.1 in Supplement S2). For hemeroby, which indicates disturbance or anthropogenic alteration of habitats, the directions of the differences were inverse, but followed the same trends. For detailed information on species establishment with respect to the corresponding donor sites, see Table S2.

Abiotic Characteristics of Donor and Recipient Sites

Within different grassland types, the productivity of donor and recipient sites was similar, with a tendency toward higher

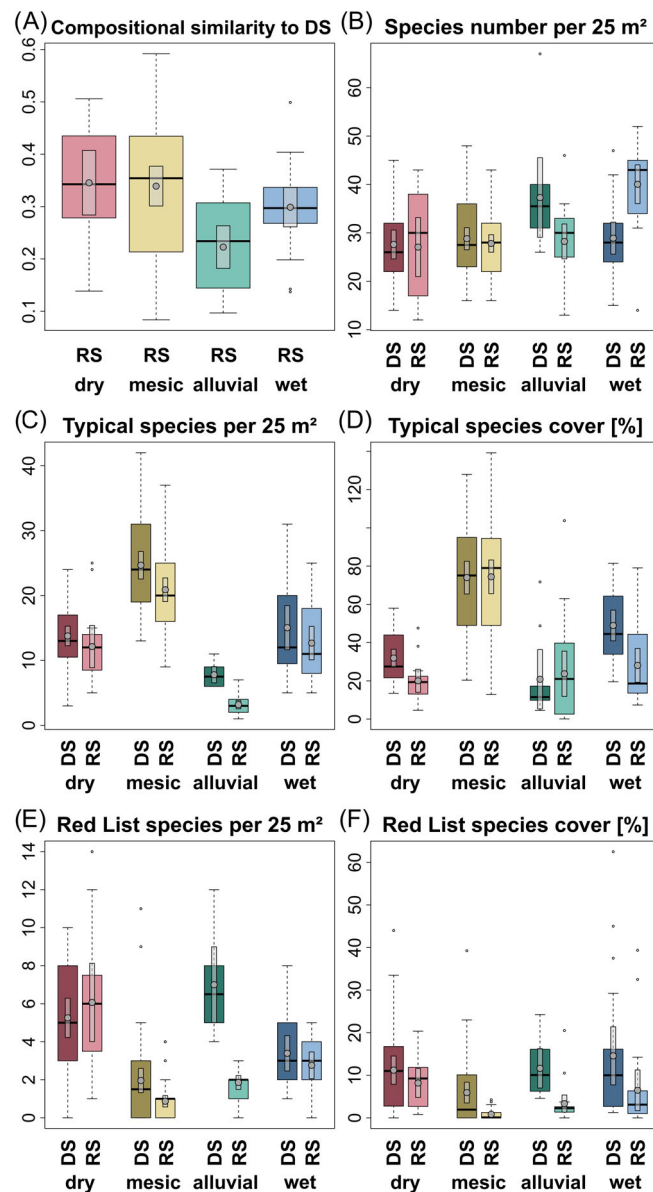


Figure 2. Restoration success on the recipient sites (RS) for the different target grassland types—dry, mesic, alluvial, and wet grasslands. In (B)–(F), data for the donor sites (DS, darker colors) are given in addition to those for the recipient sites (lighter colors). The number of plots (sites) within the grassland types (from left to right) for the donor sites is 35 (12), 50 (15), 10 (3), and 23 (7), and for the recipient Sites 15 (6), 53 (20), 21 (7), and 21 (8). The boxplots are based on the plot level. Whisker lengths are limited to 1.5 times the interquartile range. Group means are indicated by the gray points and the corresponding 95% CI by the light gray bars.

productivity of recipient sites of alluvial grasslands (Fig. 3A). Dry grasslands were less productive than the other grassland types (mean of 109.7 vs. 276.3 g/m² dry matter yield). There were trends toward lower soil organic C, higher plant-available-P, lower biomass N/K, and N/P ratios, and lower Ellenberg *F* values in the recipient sites compared with the donor sites across grassland types (Fig. 3B, 3E, & 3G–I). Soil C/N ratios, plant-available K, and soil pH values were similar between donor and recipient sites within grassland types (Fig. 3C, 3D, & 3F). The dry grasslands were characterized by more

alkaline soils than the other grassland types (mean soil pH of 7.3 vs. 5.3; Fig. 3F).

Species Composition and Grassland Type-Specific Success Factors

Dry grasslands were separated into two subgroups along the first NMDS axis, which reflected the respective soil conditions (Fig. 4A). Recipient sites on sandy substrates (nos. 4–6) and their corresponding donor sites had higher Ellenberg *L* and

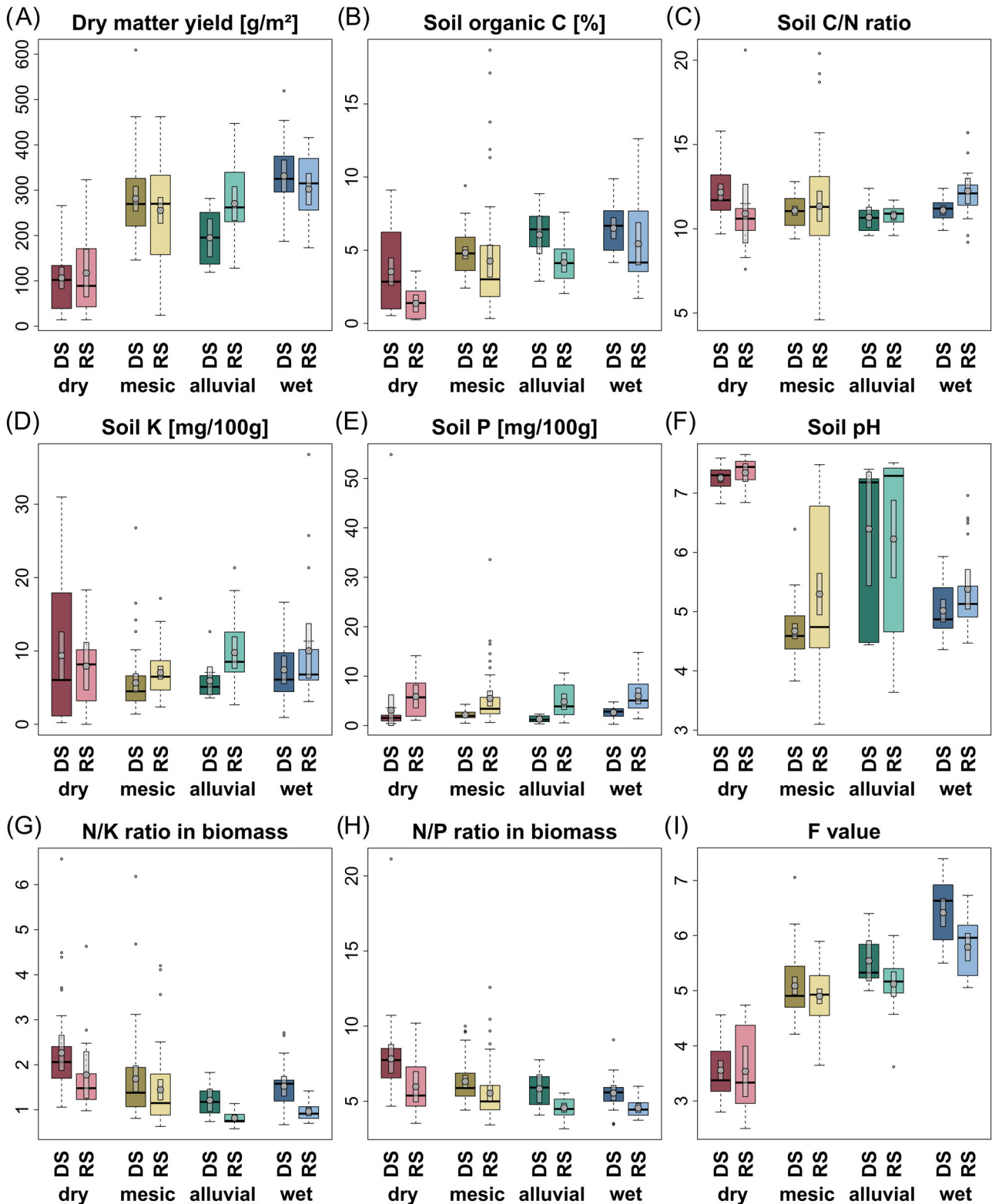


Figure 3. Productivity, abiotic conditions, and nutrient stoichiometry of the donor sites (DS, darker colors) of the different grassland types—dry, mesic, alluvial, and wet grasslands—and the corresponding recipient sites (RS, lighter colors). The number of plots (sites) for the eight groups (from left to right) is: 35 (12), 15 (6), 50 (15), 53 (20), 10 (3), 21 (7), 23 (7), 21 (8) (see Supplement S1 for missing values). The boxplots are based on the plot level. Whisker lengths are limited to 1.5 times the interquartile range. Group means are indicated by the gray points and the corresponding 95% CI by the light gray bars.

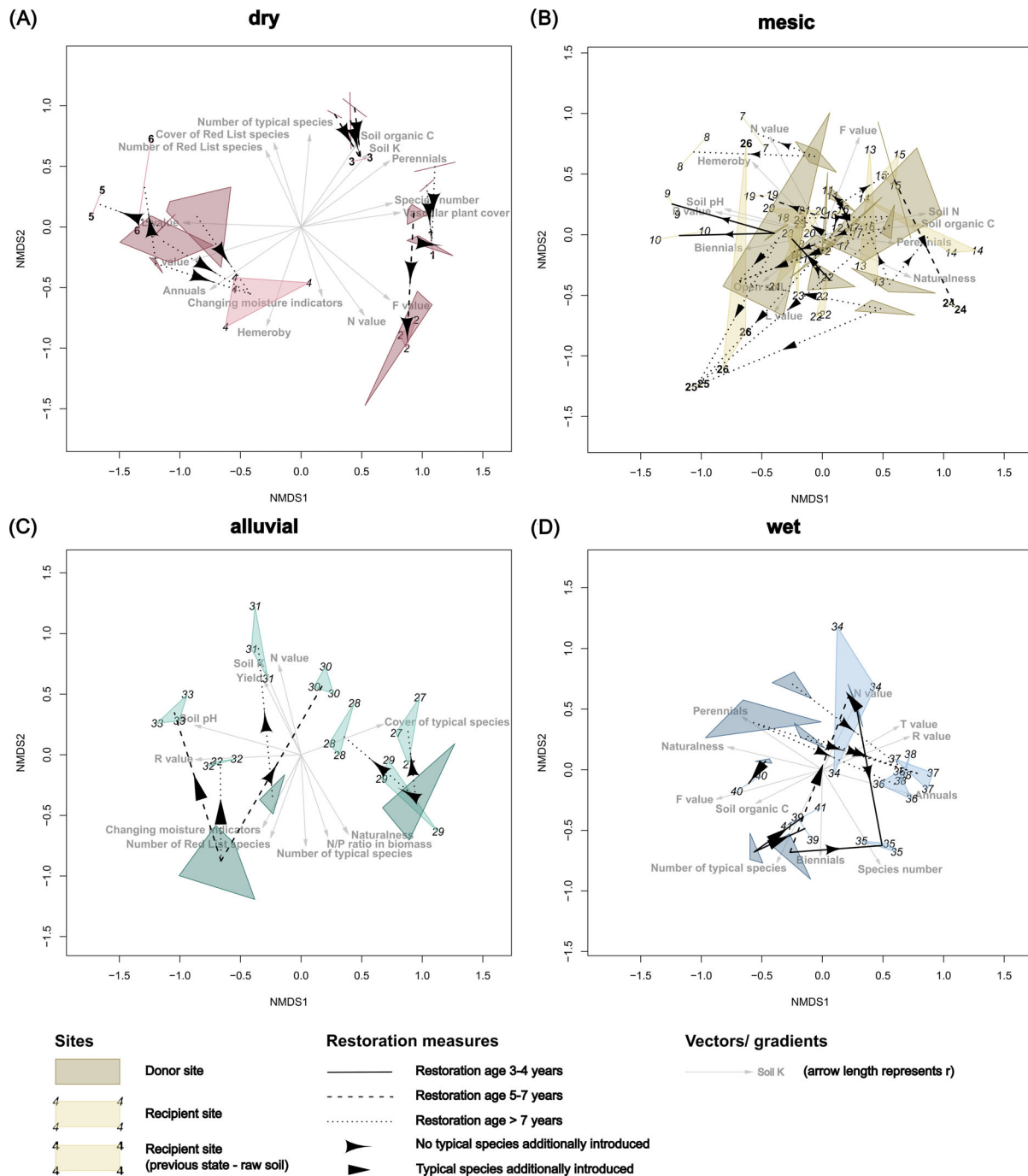


Figure 4. Two-dimensional non-metric multidimensional scaling (NMDS) ordinations for the vegetation composition of donor and recipient sites for each target grassland type (A—dry, B—mesic, C—alluvial, and D—wet). Sites are symbolized by convex polygons connecting the respective plots, additionally displaying information on the previous state and the numbering (site number at each vertex) of the recipient sites (see legend and Table S1). Black lines with arrowheads connect donor site centroids with the centroids of their corresponding recipient sites and display information on the restoration measures (restoration age was a continuous variable, categories only serve visualization; see the legend). Gray arrows indicate correlation ($r^2 \geq 0.3$) of variables of soil conditions, biomass characteristics, species characteristics, and restoration success with directions in the ordination space. For better readability, the following variables were removed despite $r^2 \geq 0.3$ due to strong correlation with other variables (in parentheses): (A) R value (perennials), cover of typical species and naturalness (number of typical species), dry matter yield and growth height (N value), soil N (soil organic C); (B) annuals and T value (biennials); (C) N/K ratio (changing moisture indicators), soil P (soil K), species number (number of typical species), growth height (soil pH), vascular plant cover (dry matter yield), hemeroby (N value); (D) monocarpic perennials (number of typical species), Ellenberg wetness indicators and soil N (F value), hemeroby (R value). Stress levels: (A) 14.0, (B) 22.4, (C) 19.0, and (D) 20.2.

T values and higher proportions of annual species. Sites on rocky substrates (nos. 1–3) contained more perennial species, had higher soil organic C contents and plant-available K, and had higher species numbers and vascular plant cover. The success variables number and cover of Red List and typical species were positively correlated with each other and with naturalness and were largely independent of the substrate. Stronger deviations in species composition (nos. 2 and 4) between donor and recipient sites were associated with a lower number and cover of Red List and typical species. In these cases, recipient sites had developed soils (no raw soils) and tended to be more productive than their corresponding donor sites, as indicated by higher Ellenberg *N* values, dry matter yield, and growth height.

The mesic grasslands differed in a range of environmental and species characteristics (e.g. plant life forms, Ellenberg *F* values, soil organic C, and soil pH) (Fig. 4B). No success variables or environmental gradients were consistently associated with the deviations in species composition between donor and recipient sites. However, several recipient sites (e.g. nos. 7–10, 19) with a species composition clearly deviating from the respective donor sites had higher hemeroby, soil pH, Ellenberg *R* and *T* values, and proportions of annual and biennial species, while naturalness and soil organic C were lower. The recipient sites no. 25 and 26, where plant material had been applied on raw soils, were particularly different from their donor sites, with pronouncedly more open soil, higher Ellenberg *L* values, and lower Ellenberg *F* values. Selection of GLMs supported the picture that more alkaline soils of recipient sites led to higher dissimilarities in species composition from donor sites. The models suggested that cover of typical species and naturalness were negatively affected, while hemeroby was increased (Table S3, Supplement S2). Raw soils on recipient sites decreased the similarity to the corresponding donor sites but were beneficial for the cover of Red List species. The selected GLMs suggested several additional links of explanatory and success variables, which did not always point in the same direction.

In alluvial grasslands, species composition of most recipient sites differed rather strongly from their corresponding donor sites (Fig. 4C). These deviations were consistently correlated with increased hemeroby, dry matter yields, Ellenberg *N* values, and plant-available soil K and P in recipient sites. At the same time, naturalness, biomass N/K and N/P ratios as well as species numbers and numbers of typical and Red List species were lower.

In wet grasslands, deviation in species composition between donor and recipient sites differed in strength and was associated with different environmental gradients and species characteristics (Fig. 4D). Some recipient sites differing strongly from their corresponding donor sites (nos. 36–38) showed lower naturalness, Ellenberg *F* values, soil organic C and N contents, and numbers of typical species. Hemeroby, Ellenberg *T* and *R* values, as well as proportions of annual species tended to be increased in recipient sites. Recipient sites no. 39–41 replicated their corresponding donor sites quite well concerning both species composition and abiotic conditions. Compared to donor sites, similar numbers and cover of typical and Red List species,

as well as similar hemeroby and naturalness, were achieved (see also Table S1).

Success Factors Across Grassland Types

The target grassland types affected restoration success concerning all response variables (Table 1). In dry grasslands, similarities of recipient sites to their corresponding donor sites were higher than in the other grassland types, with the lowest similarity in alluvial grasslands. Recipient sites of alluvial and mesic grasslands also had lower numbers of Red List species, with lowered cover of these species in mesic grasslands only. Concerning soil characteristics, higher plant-available K in recipient sites was positively associated with most success variables, except similarity to donor sites. Increased soil pH was negatively associated with the similarity to corresponding donor sites, species numbers, as well as numbers and cover of typical species, but did not affect the number and cover of Red List species. Dry matter yield increased the cover of typical species. Use of multiple donor sites was negatively associated with the numbers of typical and Red List species as well as the cover of Red List species. Numbers and cover of Red List species were increased if plant material had been applied on raw soils. The number of typical species was increased by additional introduction at restoration. Restoration age did not affect the number and cover of both typical and Red List species but was associated with decreasing total species numbers. The picture of relevant success factors outlined above was generally also found for naturalness and hemeroby, with inverse effect directions for the latter (Table S2.1 in Supplement S2).

Discussion

In our study, restoration success and its drivers varied strongly among different grassland types. While dry grasslands showed the highest restoration success due to effective creation of donor site conditions on the recipient sites, restoration success for mesic grasslands was high for common grassland species but less so for Red List species. In wet grasslands, appropriate moisture regimes were vital for the establishment of typical species and for replicating donor communities. Alluvial grasslands showed the lowest restoration success, probably due to elevated nutrient levels on these sites.

Dry Grasslands

Abiotic conditions of the donor sites were successfully replicated on four recipient sites either by depositing humus-free sand for the restoration of sandy grasslands or by topsoil removal for the restoration of grasslands on rocky substrates. The resulting raw soils provided favorable, nutrient-poor conditions and low competition for the introduced plant species (Kiehl et al. 2010). Most likely, this was decisive for the establishment of many endangered and typical species on the recipient sites (e.g. *Bassia laniflora* and *Globularia bisnagarica*). These findings are in line with literature on the restoration of dry grasslands emphasizing the reduction of soil fertility to

promote target species establishment (Gilhaus et al. 2015; Řehouňková et al. 2021).

Although success in dry grassland restoration was lower on developed soils, considerable numbers of typical and Red List species were still transferred to the recipient sites. This finding supports Storm et al. (2022) in that raw soils may be advantageous but are not a must. For example, in recipient Site no. 2, the species number and the number of Red List species were even higher than in the corresponding donor sites. The combination of two donor sites with different abiotic conditions and species compositions probably increased the chances of establishment of species. This is in line with results of Valkó et al. (2022) showing successful establishment of species-rich grasslands on former arable fields utilizing multiple donor sites.

Mesic Grasslands

Overall, restoration of mesic grasslands was successful concerning the number and cover of typical, rather common plant species (e.g. *Anthoxanthum odoratum* and *Leucanthemum vulgare* agg.). However, success with respect to Red List species was rather low. This is in line with the findings of Biro et al. (2024) and there were probably different reasons for individual species. For example, the endangered *Sanguisorba officinalis* failed to establish on recipient Sites 11–12, 15, and 17 despite coverage of 25.8% on the (common) corresponding donor site. This may be attributed to late seed maturity, as successful transfer has been reported when plant material was obtained in September/October (Harvolk-Schöning et al. 2020), while the cutting dates in our study ranged from July to (early) September. Many studies have shown that it is beneficial for species introduction and establishment to combine plant material from multiple cuts, in particular if target species have different phenologies (Bischoff et al. 2018; Valkó et al. 2022). For other Red List species, low abundance on the donor sites in combination with specific soil requirements probably hindered establishment (Wagner et al. 2021; Biro et al. 2024).

In contrast to dry grassland restoration, raw soils did not prove universally favorable in mesic grasslands. While our results show a positive effect on the cover of Red List species, similarity to donor sites was reduced. For example, at recipient Sites 25 and 26, the created abiotic conditions were too dry for many of the introduced species. This confirms practitioners' warnings that raw soils are not suitable for restoring relatively productive grasslands (Sommer et al. 2023b).

On recipient sites 7–10, which were created by topsoil deposition on road embankments, the increased Ellenberg *R* values compared to the donor sites were due to higher soil pH. In combination with increased hemeroby and reduced naturalness of the recipient sites, these results confirm that anthropogenically created and affected sites will often not be suitable to perfectly replicate semi-natural grassland communities (Tikka et al. 2000). However, the more suitable soil conditions are for the introduced species, the closer semi-natural grassland communities can be reproduced, providing an opportunity for restoration (Starr-Keddle 2011).

Alluvial Grasslands

Across our study panel, restoration of alluvial grasslands was least successful. Similarity between donor and recipient sites was lowest, and recipient sites performed worse than donor sites across all success variables, except for the cover of typical species. This was mainly due to high cover of the grass species *Alopecurus pratensis* and *Deschampsia cespitosa* on several recipient sites. Although these species are characteristic of alluvial grasslands, they are common and typically not considered target species for restoration. The low restoration success was likely caused by elevated nutrient and productivity levels on the recipient sites, irrespective of their previous land use (i.e. grasslands vs. arable fields). As a result, Red List species indicative of low nutrient availability (*N* value ≤ 2) such as *Galium boreale* or *Selinum dubium* were barely successfully transferred despite their regular presence on some donor sites. This issue is well documented in alluvial grassland restoration (Donath et al. 2007; Sommer et al. 2023a). As sufficiently low-productive recipient sites are often not available due to nutrient enrichment in Central European landscapes (Stevens et al. 2010; Schils et al. 2022), topsoil removal is a potential yet radical approach to achieve these conditions (Hölzel & Otte 2003). Alternatively, consequent biomass removal may reduce nutrient levels, too, but is time consuming (Sommer et al. 2023b).

Wet Grasslands

Our analyses indicate that in wet grasslands, similarity between recipient and donor sites was primarily driven by soil moisture, highlighting its critical role for the successful restoration of this grassland type (Breit et al. 2023). Recipient sites 39–41 show that appropriate moisture regimes promote the successful establishment of endangered and typical species such as *Carex panicea* and *Succisa pratensis*. On recipient sites where conditions were too dry compared to the donor grasslands (e.g. Sites 36–38), the additional species recorded were predominantly non-typical of wet grasslands, such as *Arrhenatherum elatius* and *Trifolium campestre*. This may reflect a deviation from the intended restoration targets. While moisture conditions have to be suitable, flooding events can limit the establishment of target species. For example, Rohal et al. (2019) found that wetland sites restored after an invasion by *Phragmites australis* had higher cover and richness of native plants where flooding frequency was lower.

Success Factors Across Grassland Types

While there were differences in drivers of restoration success between different grassland types, our results underline the general importance of abiotic matching between donor and recipient sites. Soil analyses for nutrients (e.g. phosphorus) and pH before restoration can be very helpful (Sommer et al. 2023b). Our regression models also indicated several other factors that are important for restoration success across grassland types.

Raw soils positively affected the number and cover of Red List species. In Europe, semi-natural grasslands face

substantial threats from increased fertilization and intensification of land use (Schils et al. 2022), and nitrogen enrichment from atmospheric deposition (Stevens et al. 2010). Endangered plant species often depend on low-competitive, nutrient-poor conditions (Klaus et al. 2011), which raw soils provide, thereby often enhancing abiotic matching with low-productive donor sites.

Introducing typical species in addition to transferring plant material led to higher numbers of these species establishing at the recipient sites. In some cases, this likely facilitated the establishment of species absent from the donor sites, such as *Betonica officinalis* and *S. pratensis* at recipient site 24. In other cases, it appeared to support species with low densities on donor sites, such as *S. pratensis* at site 41. This is in line with studies by Baasch et al. (2016) and Hofmann et al. (2020), which demonstrated that the additional introduction of target species enables or improves the chances of successful establishment.

Across our study panel, species richness decreased with increasing restoration age. Plant material had been mostly applied to open soils, which usually leads to initial dominance of short-lived, ruderal species (Klaus et al. 2018). These gradually diminish with the implementation of post-restoration management as gaps in the sward close (Baasch et al. 2012; Sommer et al. 2023a). Interestingly, restoration age was negatively correlated with the proportion of perennial species but positively correlated with the proportion of annual species. The main reason for this was some dry and very old recipient sites with relatively low species numbers coupled with high proportions of annual species ($\geq 25\%$). Notably, Sites 4, 5, and 6 (restoration age of 17–18 years) had a very limited specialist species pool dominated by annuals such as *B. laniflora*, *Medicago minima*, or *Silene conica*. Regression models indicate that restoration age had no significant impact on numbers and cover of Red List and typical species across all recipient sites. This supports the view that low-intensive long-term management appropriate for the respective grassland type can maintain restoration success stable over time (Waldén & Lindborg 2016; Sommer et al. 2023a).

Finally, dry matter yield was positively associated with the cover of typical species. This relationship likely reflects the relatively high productivity of many mesic recipient sites (e.g. 11, 22, and 23) combined with the substantially larger pool of species classified as typical for these grasslands compared to other types, thereby increasing typical species cover.

Limitations of the Study and Future Research Directions

Our study provides valuable insights into the success or failure of grassland restoration with plant material transfer in practice. However, investigating corresponding donor and recipient sites at a single time point after restoration is inherently coupled with some limitations in both measuring success and identifying its driving factors. These limitations can—and should—be addressed in restoration practice and science.

While many typical and endangered species on the recipient sites originated from plant material transfer or additional

introduction measures, especially the rather common plant species came, partly, also from other sources. These may include emergence from the soil diaspore bank (Klaus et al. 2018; Ludwig et al. 2021), immigration from surrounding habitats (Klinger et al. 2021; Valkó et al. 2022), and—particularly on former grasslands—previous occurrence on the sites (Sommer et al. 2023a). Since our data did not allow for separating these effects, our study pictures grassland restoration outcomes more broadly rather than isolating the success specifically attributable to plant material transfer from donor sites.

Concerning success factors, we identified several noteworthy relationships between restoration measures and outcomes. While the sample of 41 recipient sites was rather large, contributions from more than 12 project partners and regions would have been ideal, as restoration setups and site conditions were partly similar within those. However, acquisition was challenging, posing a limit to this. Further, some management actions or agricultural practices not known to us, such as fertilization, removal of undesired (e.g. poisonous) species, mowing, or grazing, likely influenced long-term species establishment on recipient sites (Klinger et al. 2025).

Despite the big advantage of directly investigating practical restoration projects, future research is needed to further support generalizability. Therefore, we advocate for more systematic studies encompassing broader site panels from diverse regions and involving a broad range of projects. Such research would greatly benefit from thorough initial documentation of restoration measures and site conditions and from monitoring by the respective practitioners. Standardized monitoring in practical restoration projects would enable meta-studies, offering deeper insights, and clearly defining the parameters by which success is measured would contribute to better comparability (Biro et al. 2024). Particularly when assessing restoration success on former grasslands, baseline data on the pre-restoration state should be collected (Biro et al. 2024). As knowledge about success factors in practical restoration grows, it will provide essential guidance for tackling the considerable challenge of restoring grassland ecosystems in the coming decades.

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Supporting Information

The following information may be found in the online version of this article:

Figure S1. Correlation coefficients of the explanatory variables tested in the model selection process for cross-grassland success factors of restoration.

Supplement S1. Deviations from default course of action and missing values.

Supplement S2. Methods and results of the analyses on naturalness and hemeroby.

Table S1. Investigated recipient sites with information on the locations, donor sites, restoration measures, site conditions, and restoration success.

Table S2. Vegetation data of the 41 recipient sites in comparison to their corresponding donor sites.

Table S3. Overview of the (generalized) linear models selected for the variables of restoration success in mesic grasslands.

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