aus dem Institut für Landschaftsökologie und Ressourcenmanagement

Professur für Landschaftsökologie und Landschaftsplanung

der Justus-Liebig-Universität Gießen

Restoring semi-natural grasslands in Central Europe with plant material transfer – achievements, success factors, and knowledge transfer

Inauguraldissertation

zur Erlangung des Grades

Doctor agriculturae (Dr. agr.)

im Fachbereich 09 – Agrarwissenschaften, Ökotrophologie und Umweltmanagement der Justus-Liebig-Universität Gießen

vorgelegt von

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Gießen, Oktober 2025

mit Genehmigung des Fachbereichs Agrarwissenschaften, Ökotrophologie und Umweltmanagement der Justus-Liebig-Universität Gießen

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Datum der Disputation: 31.10.2025

Matthias Harnisch,
City of Riedstadt

„What you do makes a difference, and you have to decide what kind of difference you want to make.“

Jane Goodall

Contents

List of publications and formal remarks

This thesis is based on the following three research articles:

Sommer, L., Klinger, Y. P., Donath, T. W., Kleinebecker, T., & Harvolk-Schöning, S. (2023). Long-term success of floodplain meadow restoration on species-poor grassland. *Frontiers in Ecology and Evolution, 10,* 1061484. https://www.frontiersin.org/articles/10.3389/fevo.2022.1061484

Sommer, L., Donath, T. W., Harvolk-Schöning, S., Kleinebecker, T., Schneider, S., Voß, N., & Klinger, Y. P. (2025). Grassland restoration practice in Central Europe: Drivers of success across a broad moisture gradient. *Restoration Ecology*, *33*(7), e70106. https://doi.org/10.1111/rec.70106

Sommer, L., Castro Campos, B., Harvolk-Schöning, S., Donath, T. W., Kleinebecker, T., & Klinger, Y. P. (2023). Grassland restoration with plant material transfer – bridging the knowledge gap between science and practice. *Global Ecology and Conservation*, *47*, e02638. https://doi.org/10.1016/j.gecco.2023.e02638

While chapter 1 is a synthesis of these articles, the articles themselves are given in chapters 2 to 4. The reference styles of the articles were aligned to the 7th edition of the Publication Manual of the American Psychological Association. Figures, tables, and supplements were re-numbered to enable identifiability across the chapters following the pattern:

- type chapter.(supplementary material)number
- e.g., Figure 2.3 – third figure in the main text body of chapter 2
- e.g., Table 4.S2 – second table in the supplementary materials of chapter 4

Supplementary materials of the different chapters which are large-formatted or have their own literature list are not provided directly in this dissertation but can be found in the original research articles – this is indicated on the respective pages.

Chapter 1: Ecological grassland restoration with plant material transfer – a synthesis

Leonhard Sommer

Introduction and objectives

In Central Europe, humans have long made use of the capacity of grazing livestock to persist on vegetation unfeasible for direct nutritional use by humans (Hartung, 2013; Hejcman et al., 2013). The microbial communities in the alimentary canals of cattle, sheep, goats, donkeys, and horses allow these animals to digest the fibre-rich fodder provided by grasslands (Bell & Burden, 2023; Leiber et al., 2014; Wunderlich et al., 2023). With the neolithic age (5500–2000 BC), humans started to clear parts of the largely forested landscapes of Central Europe for agricultural use (Hejcman et al., 2013). While the more fertile parts of the landscape were often used as arable fields, the less productive, rather dry, wet, or periodically flooded areas were often used as grasslands to feed the widely kept livestock (Luick, 2021; Partzsch, 2000). For a long time, most grassland stands were very species-rich and marked by a plethora of flowers (Hejcman et al., 2013).

With rapid population growth during the industrial revolution, agricultural practices in Central Europe changed rapidly, too, necessarily and significantly increasing total productivity (Cecil, 1979). While grasslands on marginal land were affected by abandonment (MacDonald et al., 2000; Schils et al., 2020), grasslands on better soils were often converted to arable fields (Böger, 1991; Nitsch et al., 2012) or their use was intensified. Intensification comprised melioration, fertilisation, increased cutting frequency or livestock density (Böger, 1991; Jepsen et al., 2015; Manning et al., 2015), and active sowing of improved cultivars of forage species to the grassland communities (Krautzer & Graiss, 2005; Tiemann, 1944). All this led to dramatic decline in species-richness of grasslands, usually leaving a rather small pool of competitive grass and forb species profiting from the created nutrient-rich soil conditions and altered water regimes (Böger, 1991; Francksen et al., 2022). Nowadays, food supply in Central Europe is not relying any longer on semi-natural, species-rich grasslands. While consumption of dairy products and beef is high (Bak-Filipek, 2018; Bórawski et al., 2020; Statista, n.d.-b), the animals are, to a large part, fed with maize, cereals and soy produced on arable land, partly abroad (Knaus, 2016; Nguyen et al., 2010). Those parts of the rations still originating from grasslands often stem from species-poor and highly productive stands (Bettin et al., 2020; Taube et al., 2014).

While large-scale re-extensification of grassland use in Central European agriculture seems unlikely at this point, there is societal consensus that preserving and promoting biodiversity of these ecosystems is not only desirable, but urgently necessary. Various types of species-rich, semi-natural grasslands have been taken under far-reaching conservation status with the Habitats Directive of the European Union (Council Directive 92/43/EEC, 2013). With the Nature Restoration Law, pronounced focus lies on active recreation of these habitats (Regulation (EU) 2024/1991). Appropriate, low-intensive post-restoration agricultural use or – as a replacement – non-agricultural management is a precondition for success of such efforts (Rasran et al., 2007; P. Török et al., 2011). However, impoverished soil diaspore banks (Bekker et al., 1997; Hölzel & Otte, 2004) and lacking or very slow immigration of target plant species from the surroundings (Donath et al., 2003) often demand active species introduction. Besides targeted propagation and sowing or planting of species to restore semi-natural grassland communities, direct harvest of diaspores from species-rich donor grassland sites at seed maturity of a large proportion of species is a commonly used approach (Kiehl et al., 2010; P. Török et al., 2011).

In diaspore collection for grassland restoration, the most common methods of direct harvest are threshing, brush-harvesting, and mowing (Kiehl et al., 2010). In case of the latter, the diaspore-containing plant material can be transferred to the recipient sites either in dried form (hay) or freshly (Figure 1.1). As a major advantage, with fresh material, not only diaspores of vascular plants are usually transferred, but also living invertebrates (Stöckli et al., 2021) and diaspores of cryptogams scratched from the soil surface by raking (Eichberg et al., 2010; Michalska-Hejduk et al., 2017). Another benefit is the protective effect of the plant material layer on seedlings in case of drought after application (Eckstein & Donath, 2005). When grassland stands on the donor sites are very low-growing, for example in case of extremely nutrient-poor sandy grasslands, plant material is sometimes collected just by raking, without a preceding cutting step (Eichberg et al., 2010). Plant material transfer was proven to be a potentially effective method in restoring species-rich grassland communities of dry (Kiehl et al., 2006; Storm et al., 2022), mesic (Baasch et al., 2016; Wagner et al., 2020), and wet conditions (Klimkowska et al., 2010; Rasran et al., 2007), and of alluvial conditions with alternating moisture regimes (Baasch et al., 2016; Harvolk-Schöning et al., 2020).

Figure 1.1: Application of freshly cut plant material collected from a species-rich donor site on a recipient site at the Northern Upper Rhine (Hesse, Germany) in 2006. In the back part of the photo, the soil had been disturbed to lower competition for the introduced plant species. Photo: Matthias Harnisch, City of Riedstadt.

Over several decades, science has collected valuable knowledge on factors influencing success of grassland restoration with plant material transfer. Among those, there were, for example, soil preparation (Poschlod & Biewer, 2005; Schmiede et al., 2012), soil conditions (P. Török et al., 2011), or combination of plant material transfer with other seed introduction methods (Baasch et al., 2016; Hofmann et al., 2020). However, at the start of this thesis, there were clear knowledge gaps, too. Long-term success of restoration measures had been barely investigated, along with the long-term effects of success factors considered crucial, such as soil preparation. At the same time, it was not clear how well restoration worked in "practical" projects focussing rather on grassland restoration itself than on answering specific research questions. In combination with this, it was not known if practitioners applied the scientific knowledge in their projects, and which success factors not focused by ecological science so far were additionally important in practice. With three studies, the aim was to fill these knowledge gaps, and the research articles that emerged from this work are presented in chapters 2 to 4 of this thesis.

Chapter 2 deals with the long-term success of floodplain meadow restoration in a large field trial at the Northern Upper Rhine in Hesse, Germany (Figure 1.3). Species were introduced via transfer of plant material harvested on species-rich donor sites, and different soil preparation treatments were tested on the 20 species-poor grassland sites chosen for restoration. The sites were revisited in the year 2021, 13-16 years after plant material transfer (Figure 1.2), to compare the vegetation composition and feeding value of the recipient sites to that of the donor sites. Soil and biomass analyses as well as modelling of the water regime supported identification of factors explaining the observed levels of restoration success.

Figure 1.2: Vegetation plot (25 m²) at the Northern Upper Rhine during the field season in 2021.

Chapter 3 deals with success of practice projects. In 2021 and 2022, 41 recipient sites of plant material transfer were investigated along with their corresponding donor sites across Germany and Luxembourg (Figure 1.3). The sites comprised dry, mesic, alluvial, and wet grasslands and covered a broad timespan since restoration (3-18 years). Soil and biomass sampling, along with detailed information from the project partners on the restoration measures and setups, were used as a basis for analysing the drivers of restoration success.

Chapter 4 collects the views and knowledge of 33 practitioners from Germany, Luxembourg, and Switzerland (Figure 1.3) on crucial success factors of grassland restoration with plant material transfer. A framework is developed ordering the success factors and their complex relationships according to the process plant material transfer. The findings are compared with knowledge in the European scientific literature on the topic to find out to which degree practitioners apply the scientific evidence in their projects and if science considers the questions relevant for practitioners. In this synthesis chapter, the overarching findings of the three studies are presented and discussed.

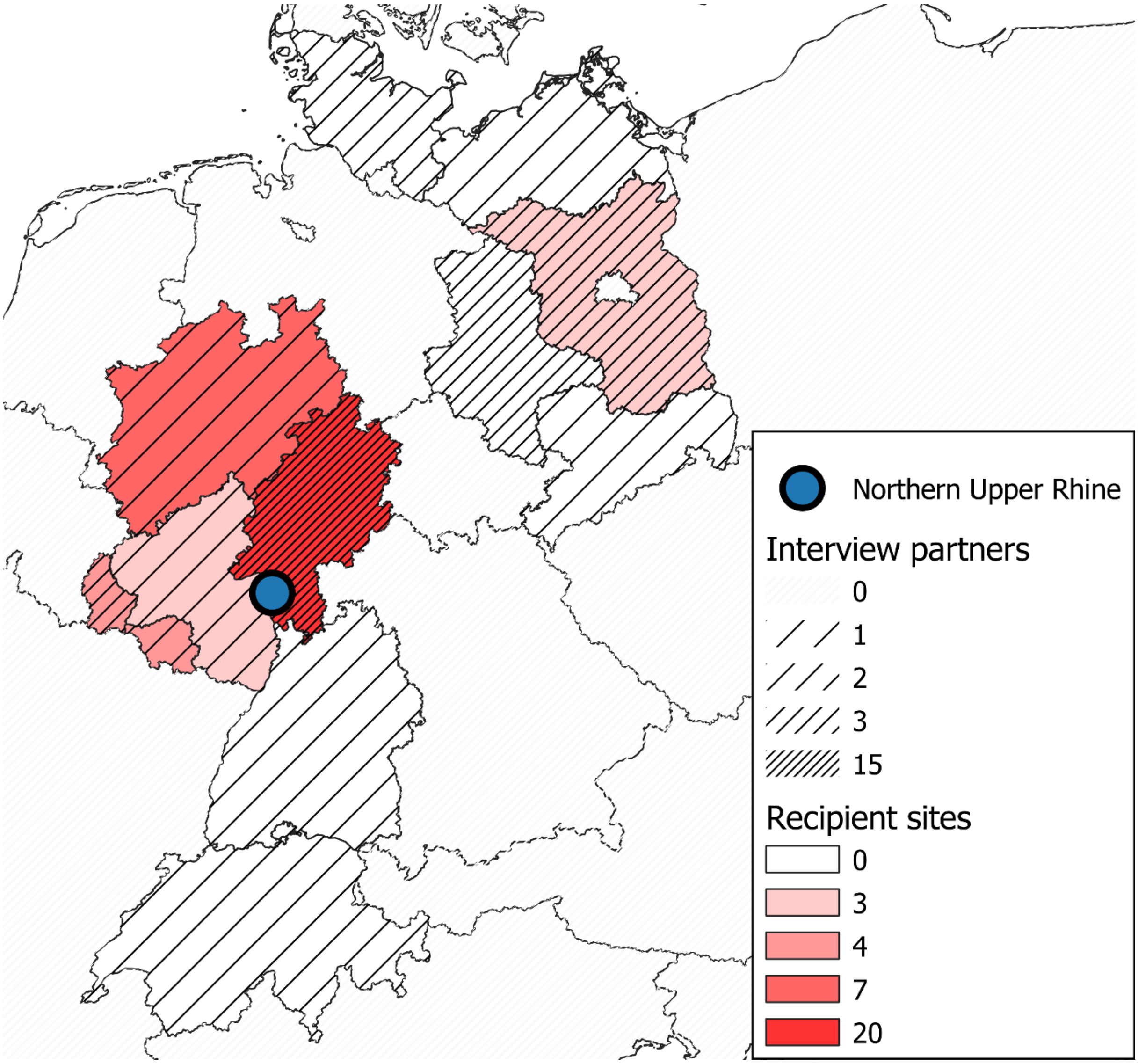

Figure 1.3: Number of interview partners (chapter 4) and recipient sites (chapter 3) per state or federal country (for Germany) and location of the study region at the Northern Upper Rhine (chapter 2). Source geodata from *Countries - Eurostat* (n.d.) and BKG (2025).

Main results and conclusions

In the following, I present a cross-study synthesis of the findings on the identified main success factors for grassland restoration with plant material transfer. Supported by further literature, conclusive recommendations for restoration practice are given.

Abiotic factors are key for restoration success

Abiotic suitability of recipient sites to support the target plant communities was identified and confirmed as a major precondition for successful grassland restoration with plant material transfer across all three studies.

Many of the interviewed practitioners raised the topic of abiotic conditions, stressing different aspects as relevant for success in their respective projects (chapter 4). Findings in European scientific research largely aligned with the practitioners' experiences and views (chapter 4), and the grassland investigations of this thesis further supported them (chapters 2 and 3). Generally, abiotic matching of recipient and donor sites of plant material transfer was confirmed as an important success factor. Species composition shifts and failures of species transfer reflected abiotic differences between recipient and donor sites regarding soil nutrient levels and productivity, soil pH, or water regime.

Too high nutrient levels and productivity of the recipient sites hampered restoration success in many cases (chapters 2 and 3; Figure 1.4). This success factor is continuously confirmed by grassland restoration research (Dullau et al., 2023) and addressed in compendiums on the topic (DVL e. V., 2025). In the studies of this thesis, it proved particularly relevant in restoration of alluvial grasslands. Even over long periods (≥ 13 years, chapter 2), nutrient levels and productivity kept determining the species composition of the restored plant communities. This underlines the significance of ensuring sufficiently low productivity at the outset of a restoration project, in contrast to the notion of creating those conditions post-restoration by management, which is sometimes expressed in practice, e.g., in my current working environment.

While soil analyses of donor and recipient sites are generally desirable to compare levels of individual nutrients, simpler considerations can already be very helpful in practice. In accordance with the "Law of the minimum" (Scharrer, 1949), grassland restoration research has shown the importance of nutrient ratios with respect to total biomass yield and thus competition for target plant species (Donath et al., 2007; Oelmann et al., 2009; Van de Riet et al., 2010). Given that biomass yield as an "aggregated" indicator of nutrient supply is often a crucial success determinant (chapter 2), practitioners should definitely compare the yield of a potential recipient site to that of the designated donor site(s). From my personal perception, even in case of non-grassland recipient sites (e.g., arable fields), where direct yield comparison to donor sites is not applicable, growth optics of the crops (dense/ sparse) can give an idea of the suitability for establishing target grassland communities. For cases where recipient sites are too productive, topsoil removal or more time-consuming nutrient removal by management prior to plant material transfer are recommended in all three studies. However, if agricultural use is foreseen in post-restoration management, productivity levels should not be reduced too strongly (see section "Feeding value, yield, and local farming conditions determine options for post-restoration use" of this chapter).

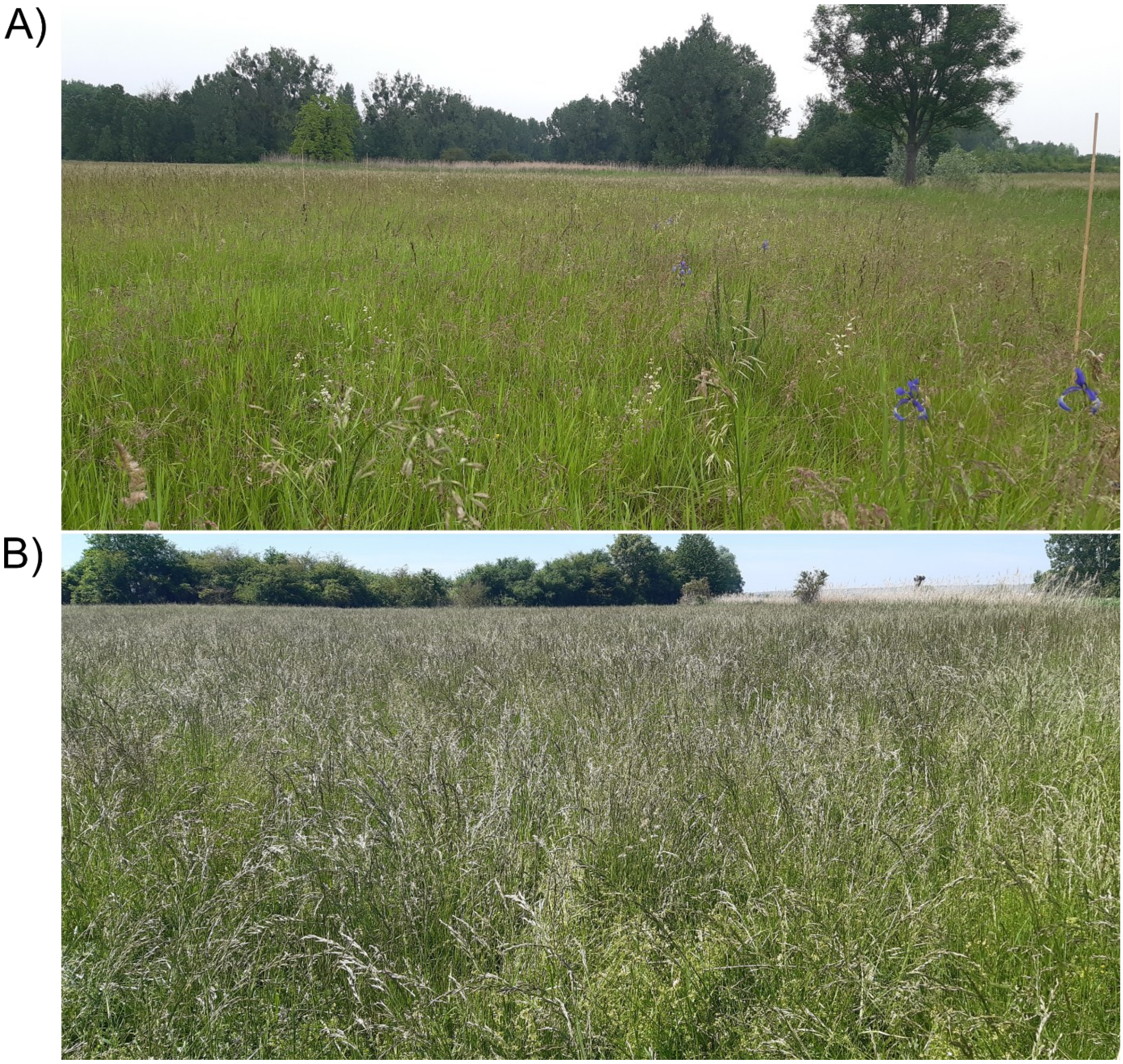

Figure 1.4: Two recipient sites of restoration at the Northern Upper Rhine with different productivity levels. A) A rather low-productive site with many successfully established individuals of endangered *Iris spuria* 15 years after plant material application. B) A very high-yielding site. 13 years after restoration, endangered target species were barely found and high cover of common grasses and herbs such as *Arrhenatherum elatius*, *Festuca arundinacea*, and *Galium mollugo* agg. was observed.

Supporting the practitioners' views and existing scientific evidence (chapter 4), water regime was proven important for restoration success of floodplain meadows with alternating moisture conditions (chapter 2) and for permanently wet grasslands (chapter 3). If in practice, maps on inundation frequencies and groundwater levels in a floodplain are not available, elevation levels of potential recipient sites can be compared to those of the donor sites as a rough predictor (Liuzzo et al., 2019; Van Eck et al., 2004). Generally, Ellenberg moisture indicator values (Ellenberg, 2001) of the existing plant species pool on donor and potential recipient sites should be compared as a proxy for soil moisture and flooding regime.

Previous land use and state affect abiotic conditions and competition

Previous use and state of recipient sites has far-reaching consequences for their capacity to support target plant communities. Competition by extant vegetation and abiotic conditions are strongly dependent on it, often raising the question of altering these conditions by substrate application or removal.

Species introduction into existing, species-poor grasslands was considered challenging by many practitioners due to competition from the extant vegetation (chapter 4). Indeed, restoration success across the 20 formerly species-poor grassland sites at the Northern Upper Rhine was only moderate (chapter 2). In contrast, restoration on arable fields and, even more, on raw soils without noteworthy competition was seen as much easier by the practitioners (chapter 4). In the study across grassland types, the positive effect of raw soils on later number and cover of endangered plant species on the recipient sites was clearly shown (chapter 3), supporting the practitioners' judgments. However, some care is advised, as topsoil removal often exposes soil horizons with lower organic matter contents (Amelung et al., 2018; Kempen et al., 2011), with negative consequences for soil functions such as water availability (Amelung et al., 2018; Huntington, 2005). For soils above bedrock, the depth of the soil column is often reduced by a large proportion, thus not only creating nutrient-poor and low-competitive, but also very dry conditions. Accordingly, in mesic grasslands, which rely on a certain level of water supply and biomass productivity even in good, near-natural state, raw soils obtained via topsoil excavation resulted in divergence of plant communities from the target states (chapter 3).

Soil preparation is important for initial species establishment

Adequate site and soil preparation is usually considered very important in grassland restoration with species introduction. While the findings of this thesis may raise some doubt about necessity in the long-term, this view was generally supported.

In line with European scientific research, many practitioners considered soil preparation helpful in achieving grassland restoration targets (chapter 4). The main goals were reducing competition by extant vegetation and preparing a seedbed to promote germination of the species introduced with the plant material. Sward disturbance had indeed promoted target species establishment in floodplain meadow restoration on formerly species-poor grasslands at the Northern Upper Rhine initially (Schmiede et al., 2012). Interestingly, the effect had disappeared 12-13 years later, with several target species obviously having emerged with some delay without soil preparation (chapter 2). However, as at the least, quicker species establishment can improve acceptance by the public, these results should not question the recommendation of preparing a site and its soil surface accordingly prior to plant material application (DVL e. V., 2025). Recognising the complaint by one farmer about long-term problems in mowing a previously ploughed recipient site (chapter 4) and the fact that an even soil surface is generally desired in modern grassland farming (Iepema et al., 2020; Mocanu et al., 2019), the recommendation to consider adequate levelling is repeated here.

Timing and approach of harvest define the transferable species pool

Optimising the collection of diaspores is a challenging but crucial task in grassland restoration with plant material transfer. Harvest date proved central as a result of the three studies. Additional species introduction should generally be considered.

A range of practitioners stressed the necessity of harvesting plant material from a high-quality donor site at the right time point and of minimising seed losses, which was supported by scientific literature on the topic (chapter 4). As the range of flowering time and seed maturity among grassland species is considerable and may increase with species-richness (Wolf et al., 2017), choosing a harvest date inevitably filters the species pool transferable from a donor site. Accordingly, the studies of this thesis revealed cases where important target species such as *Succisa pratensis* (floodplain meadows, chapter 2) and *Sanguisorba officinalis* (mesic grasslands, chapter 3) were probably not transferred due to lack of ripe seeds at the respective harvest dates. Accordingly, all three studies contain recommendations to use multiple donor sites or to harvest at more than one date, although this increases organisational complexity of restoration.

An attractive and easy approach to use the advantages of plant material transfer (e.g., invertebrate transfer, seedling protection) without only introducing a rather limited plant species pool is to combine the method with planting or with additional sowing of low-volume seed material. Species lacking on the donor site or not ripe at plant material harvest were added by some practitioners in the form of seeds from hand-collection or propagation, threshed material, or brush-harvested material (chapter 4). In accordance with the existing scientific evidence (chapter 4), the positive effect of additional introduction of typical species on their numbers later detectable on the recipient sites was statistically confirmed across grassland types (chapter 3). Additional species introduction supplementing the plant material species pool is therefore clearly recommended (DVL e. V., 2025).

Feeding value, yield, and local farming conditions determine options for post-restoration use

With respect to long-term conservation and acceptance of restoration, low-intensive agricultural use of restored grassland sites is desirable. However, as this will only work for relatively productive grassland types and in regions with an according farming structure, other solutions often have to be developed.

Many of the interviewed practitioners raised the topic of post-restoration management of recipient sites with regard to project success and thus confirmed scientific consensus on its importance (chapter 4). Long-term suitability of the biomass from restored floodplain meadows concerning yield and energy content for feeding of horses and, partly, cows and calves at the Northern Upper Rhine was a central result of this thesis (chapter 2). Indeed, all twenty recipient sites investigated in that study were under actual, low-intensive agricultural use, which stabilised the number and cover of the introduced target species in the long-term. Restoration age did barely affect the success variables across grassland types and regions (chapter 2), which was certainly grace to appropriate long-term management of most of the restored sites.

On the large scale, management of restored semi-natural grasslands will clearly face the same conditions and obstacles as management of such grasslands does in general. Given the present structural situation in Central European food supply and agriculture (see the Introduction), integrating semi-natural grasslands in farming systems remains a challenge (Gabryszuk et al., 2021; Rábek et al., 2022) and probably depends on targeted governance (Shipley et al., 2024). Accordingly, as became clear from the practitioner interviews (chapter 4), locally adapted solutions have to be developed for each grassland restoration project. For example, not only but particularly in regions with low density of grazing livestock, such as large parts of Eastern Germany (Statista, n.d.-a, n.d.-c), voluntary nature conservation and specialised landscape management companies play an important role in maintaining old and restored semi-natural grasslands (Landschaftspflegeverband Harz e.V., n.d.; NABU-Stiftung, n.d.). Partly, grassland management is refinanced by targeted marketing of meat and other products, such as in different grazing projects along the river Elbe in Saxony-Anhalt, Germany (Figure 1.5; NABU-Kreisverband Stendal, 2024; Primigenius gGmbH, n.d.). Accordingly, such models are at the transition to agricultural use. Across regions, grassland-resembling sites under public low-intensive management, such as road embankments or dykes, provide valuable opportunities for establishing species-rich communities, although organisational challenges concerning plant material application and topsoil deposition have to be met (chapters 3 and 4).

Figure 1.5: Water buffalos kept for grassland preservation in the floodplain of the river Elbe near Stendal (Saxony-Anhalt, Germany). Photo: Dr. Peter Neuhäuser, NABU-Kreisverband Stendal.

Overarching factors complete the understanding of success or failure

The three studies of this thesis made clear that a range of success factors is relevant at different stages of the process of grassland restoration with plant material transfer. The practitioner interviews showed that several overarching factors (e.g., organisation, experience levels) strongly influence the different stages of the restoration process and the restoration outcomes.

The grassland investigations for this thesis revealed a mixed picture of success in the different grassland restoration projects, and less successful outcomes were often attributable to one or more of the factors addressed in the previous sections of this synthesis (chapters 2 and 3). A key finding is that these process-related success factors are strongly influenced by overarching factors only identifiable by means of socio-ecological research approaches (chapter 4). These factors were the available resources, project organisation, intra- and interpersonal factors, and knowledge and experience levels. The interplay of process-related and overarching factors is demonstrated in the following by the examples of three investigated recipient sites (nos. 7, 8, and 30, see Table 3.S1 and Table 3.S2 of chapter 3). The observed restoration success is linked to information obtained from the interviews with the practitioners (AUTH6 and PFPO1, see chapter 4) who planned and coordinated the restoration measures.

With respect to recipient sites 7 and 8, which were located on road embankments, AUTH6 reported the following restoration goal: "*We wanted to support the [populations of the butterfly genus] Maculinea [in the river valley]. For those, Sanguisorba officinalis is important, and the donor sites contained [this plant species]. Our goal was to transfer it [to the recipient sites].*" Vegetation recording for this thesis revealed that on the donor site, *Sanguisorba* was relatively frequent. The species was transferred, but only to a very small degree. AUTH6 had obtained seed-containing hay bales from the farmer using the donor site. He explained: "*It is hard to hit the right time point [for harvest]. […] We transferred some individuals [of Sanguisorba officinalis] but worked with additional sowing in later projects*". It can be concluded that in this project, the low experience level of AUTH6 prevented a more successful outcome, as additional sowing of *Sanguisorba officinalis* or hitting a better time point for harvest would probably have supported establishment of this important target species.

On recipient site 30, PFPO1 wanted to improve the ecological status of a species-poor meadow towards a species-rich floodplain meadow. Vegetation recording revealed that this failed almost completely, as none of the typical and endangered species present on the donor site (e.g., *Iris spuria, Lotus maritimus, Ranunculus polyanthemos*) were recorded in noteworthy abundances on the recipient site. One reason surely was that the soil was too nutrient-rich, as the biomass yield was 40 % higher than that of the donor site. Additionally, in the interview, PFPO1 reported: "*Bit by bit, plant material transfer was carried out from mid-October till mid-November. The distance [between the donor and the recipient site] but also personal reasons of the implementer were the reasons that this took so long. Over that period, the plant material was lying around on the donor site […] Surely, a lot [of seeds] got lost, the material became wet in the meantime. These were surely not the best preconditions.*" It is likely that with better knowledge and higher experience, PFPO1 would have foreseen the non-optimal abiotic conditions of the chosen recipient site and used a more suitable one, or he would have considered nutrient reduction by management or topsoil removal. Furthermore, with a stronger regional network, he possibly could have acquired an implementer to step in to accelerate transfer and to avoid the seed losses that contributed to project failure.

The described examples demonstrate that linking success or failure of grassland restoration projects with plant material transfer only to process-related factors such as abiotic site conditions, plant material harvest, or additional species introduction is too simplistic to comprehensively advice practitioners on the topic. To overcome the limitations often hampering success of grassland restoration projects with plant material transfer, the importance of experienced local and regional networks, of good communication within the project team, and of trustful relationships with stakeholders is underlined in chapter 4. Furthermore, intense knowledge transfer between practitioners and between science and practice is advocated.

Future prospects

As outlined in the Introduction and objectives, the dramatic current situation of semi-natural grasslands in Central Europe, together with European legislation, clearly lays out the societal task of large-scale and impactful protection and restoration of these ecosystems. Therefore, suitable restoration methods such as plant material transfer and key success factors need to become standard knowledge among responsible authorities, organisations, and companies. In the coming years, it will be crucial to spread such knowledge by ongoing integration of new scientific findings in compendiums and guidelines, preferably in national languages (e.g., DVL e. V., 2025; Jongepierová & Poková, 2006; Kelemen & Mizsei, 2025), and by conduction of workshops and information events directed to the mentioned groups (chapter 4). To further improve the understanding of success factors of grassland restoration, supra-regional studies of practical projects explaining long-term restoration outcomes by “process-oriented” and by “overarching” factors will be of great interest. The possibilities of “classical” grassland monitoring studies and quantitative data analysis approaches should, wherever possible, be combined with the strengths of socio-ecological research methods. With this thesis, it has become apparent that this combination can be key for science to obtaining a holistic view of successful grassland restoration and to optimally support practitioners in mastering the restoration task in the coming decades.

As a final consideration, I want to point to the implications of accelerating climate change for grassland conservation and restoration in the decades to come, as issue of increasing attention in Europe and globally (Gibson & Newman, 2019; Lyons et al., 2023; Soussana & Duru, 2007). Challenged by the high level of uncertainty about the exact climatic developments to expect, extensive research has been undertaken to somewhat predict species survivorship in grasslands worldwide (Bütof et al., 2012; Gibson & Newman, 2019; Smith et al., 2017), with dramatic projections in the more pessimistic scenarios (Kane et al., 2017). Besides the question of necessary management adaptations (Chang et al., 2017; Wieden, 2003), an important but controversial issue will be the choice of propagule sources for restoration (Gibson & Newman, 2019). The idea of assisting migration of expectedly better adapted genotypes and species under future climate conditions may seem appealing to maintain grassland resilience and ecosystem services, but might overlook other local factors influencing the fitness of species in a habitat (Bucharova, 2017). For this reason, in Central European countries, the general attitude and, partly, the legislative frame favour local seed sources over non-local ones, and more research on the feasibility of both under changing climate is demanded (Skowronek et al., 2023; K. Török et al., 2024). Already noticeable problems in restoration related to climate change reported by practitioners were plant material and seed availability as well as post-transfer seedling survival under the impacts of stochastic weather events (chapter 4; Figure 1.6). Within the methods of using local seed sources, plant material transfer may be promising under the increasing drought frequency due to the positive effect of the plant material layer on seedling survival (Eckstein & Donath, 2005). However, at the same time, practitioners reported lowered willingness of farmers to forgo haymaking for plant material transfer under drought-related yield decline (chapter 4). This may, in contrast, favour the use of threshed, brush-harvested, or propagated seed material so that the hay is largely left for livestock feeding.

Figure 1.6: *Iris sibirica* with small capsular fruits and only few, probably low-fertile seeds due to drought in July 2022 in the floodplain of the river Elbe near Stendal (Saxony-Anhalt, Germany). Photo: Dr. Peter Neuhäuser, NABU-Kreisverband Stendal.

For the time being, a feasible strategy in restoration is surely to introduce a high number of native plant species from local or regional sources. These should cover a spectrum of site requirements while ensuring a large gene pool within each species, e.g., by combining multiple donor sites and cutting dates. Depending on the visible impacts of climate change on semi-natural grassland communities in the coming decades, the debate on opening grassland restoration for non-local seed sources might become more intense. Science should support the process by investigating chances and pitfalls. In particular, the performance of locally and non-locally sourced plants under experimentally altered climate conditions should be compared, and effects of sourcing on organisms on other trophic levels, such as herbivorous insects, should be investigated (Bucharova, 2017; Bucharova et al., 2016). However, a much broader dialogue on the ethics and acceptance of assisted migration must be conducted as conservation and restoration are strongly influenced by emotional attachment of people to the concept of locality and nativeness (Körner, 2019). Once more, for science as one future party in this dialogue, this strengthens the case for complementing restoration research with socio-ecological methodology.

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Chapter 2: Long-term success of floodplain meadow restoration on species-poor grassland

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2023, *Frontiers in Ecology and Evolution*, 10, 1061484. doi: 10.3389/fevo.2022.1061484

Abstract

Restoration of floodplain meadows remains a challenge, as many degraded sites suffer from seed limitation. The transfer of seed-containing plant material from species-rich donor sites is a widely used method to restore semi-natural grasslands. However, most studies on the success of such restoration projects comprise limited time frames. As factors determining restoration success may only become evident after many years, long-term observations are crucial. We re-investigated 20 restored grassland sites in the floodplain of the Northern Upper Rhine 13-16 years after plant material transfer with different soil preparation treatments. To this end, we carried out vegetation surveys on 254 permanent plots and studied the potential influence of soil preparation, soil nutrients, and hydrology on plant species composition, diversity, and transfer of target species. Since sustainable agricultural use is important to ensure the long-term stability of restored semi-natural grasslands, we further investigated biomass productivity and feeding value.

While most target species increased in frequency or remained stable over time, we found no positive long-term effect of soil preparation on vegetation development and target species establishment. Instead, increased biomass yield and flooding frequency led to reduced restoration success, while higher soil C/N ratios had a positive effect. Overall, restoration measures did not affect the agricultural value of the restored grasslands, which had higher dry matter biomass yields compared with the donor sites.

Our results indicate that the positive effect of soil preparation on the number and cover of target species, which is regularly reported in short-term studies, diminishes over time and other factors such as site conditions become increasingly important. Furthermore, additional plant material transfer or manual seeding may be necessary to support target species establishment. Concerning agricultural usability, the integration of restored floodplain meadows in farming systems is possible and can ensure long-term management and thus stability of these ecosystems. Our study shows that long-term monitoring of restoration projects is necessary, as factors determining restoration success may only become evident in the long-term.

Keywords

conservation, farming, feeding value, green hay transfer, plant material transfer, seed limitation, soil disturbance

Introduction

The worldwide degradation of ecosystems is one of the most urgent problems of our time (Díaz et al., 2019). Ecological restoration is a major tool to counteract ecosystem degradation, helping the health, integrity and sustainability of ecosystems to recover (IPBES, 2019; SER, 2004). The current UN "Decade on ecosystem restoration" (UN General Assembly, 2019) underpins the increasing importance of this field. Growing focus is given to the conservation and restoration of grasslands, as they cover a large proportion of land surface and provide high capacity to support biodiversity, multiple ecosystem services and are integral to human well-being (Bardgett et al., 2021). In Central Europe, semi-natural grasslands are of particular importance. They are the result of centuries of human activity, and low-intensive management by mowing or grazing is required to restore and maintain these semi-natural ecosystems and the services they provide (Bakker, 1989; Hejcman et al., 2013).

Floodplain meadows are outstandingly diverse grassland ecosystems with many rare and endangered plant species (Rodwell, 1992; Wesche et al., 2012). Historically, due to their high productivity, they served as an important source for forage provision for livestock (Rothero et al., 2016). Over the last decades, massive structural changes in agriculture resulted in severe consequences for floodplain meadows (Jefferson & Pinches, 2009). Conversion to arable fields, fertilization, higher cutting frequencies, and alterations of the hydrological conditions have led to a drastic decline both in the amount of floodplain meadows and their ecological quality (Bissels et al., 2004; Böger, 1991; Joyce & Wade, 1998). The restoration of the plant diversity of floodplain meadows is therefore urgent, but is a challenging and long-lasting process (Engst et al., 2016).

The mere return to low-intensive management on degraded floodplain meadows often fails, as typical plant species hardly re-establish spontaneously. This is due to the transient soil seed bank of many typical floodplain meadow species (Bekker et al., 2000; Hölzel & Otte, 2004a) and lacking connectivity to the few species-rich remnant populations (Bissels et al., 2004; Donath et al., 2003). Therefore, active diaspore introduction is required to re-establish the typical vegetation within a reasonable timespan (Bissels et al., 2004; Jõgar & Moora, 2008; Ludewig et al., 2021; Vécrin et al., 2007). Research projects have shown the suitability of active species introduction for grassland restoration (Kiehl et al., 2010). Out of the available methods, the transfer of freshly cut plant material is considered particularly advantageous with respect to genetic diversity and autochthonism, and additionally enables the transfer of organisms other than plants, such as invertebrates (Harnisch et al., 2014; Stöckli et al., 2021).

Generally, the restoration of species-rich grassland using freshly cut plant material is more challenging on species-poor grassland sites compared to arable fields or raw soils (Hansen et al., 2022; Kiehl et al., 2010; Valkó et al., 2022). Soil preparation is commonly regarded as an important prerequisite for successful target species introduction. While it reduces competition by the existing grassland vegetation and creates niches for germination and successful establishment of seedlings with low competitive power (Schmiede et al., 2012), there is increasing evidence that its positive effects can diminish over longer time periods (Freitag et al., 2021; Harvolk-Schöning et al., 2020). This affirms the importance of long-term monitoring to evaluate the success of restoration measures (Resch et al., 2019), as well as considering a range of driving factors (Hölzel, 2019).

However, in addition to restoration, semi-natural grasslands require adapted management to create adequate disturbance regimes and to overcome seed limitation (Klinger et al., 2021). Typically, management of floodplain meadows consists of mowing, which was traditionally complemented by grazing in some areas (Kapfer, 2010). To ensure an adequate management, farmers often receive subsidies as part of agri-environment schemes (Donath et al., 2021; EEA, 2022). However, the acceptance for low-intensity management practices might be increased if the biomass produced on these sites could be used profitably. Thus it is desirable to keep floodplain meadows integrated in the regional farming systems (Donath et al., 2015; Tallowin & Jefferson, 1999). This was commonly the case until the middle of the last century, but with more possibilities to increase productivity, e.g. by fertiliser input, the interest of farmers to continue this practice decreased (Hejcman et al., 2013). If it could be shown that species diversity and composition had neutral or positive effects on fodder quantity and/ or quality, this might increase the motivation of farmers to re-establish the management of sites with high nature conservation value (Donath et al., 2015). Donath et al. (2015) found that in comparison to sites with low nature conservation value, the fodder quality was comparable or even higher in sites with high nature conservation value, and that the harvested material could be integrated in farming systems. If this were the case also for restored semi-natural grasslands, a sustainable management of these sites and thus long-term restoration success could be ensured easier.

Soil conditions and productivity of floodplain meadows are linked to their agricultural value, which may consequently result in a conflict of goals for any restoration efforts (Donath et al., 2015). Increased nutrient levels can hamper the establishment of target species (Gough & Marrs, 1990; Pywell et al., 2006; Waldén & Lindborg, 2016), but relevant nutrients and respective thresholds vary between study systems. In addition, nutrient stoichiometry can modify restoration outcomes, as e.g. limitation by nitrogen (N) has been shown to compensate for negative impacts of high P and K availability, restricting productivity and species competition (Donath et al., 2007; Pywell et al., 2002). Additionally, hydrological conditions such as flood and drought frequencies can strongly affect species composition in floodplains (Hölzel, 1999; Mathar et al., 2015), but their impact on restoration success has barely been studied so far.

In a large-scale floodplain meadow restoration experiment with plant material transfer at the Northern Upper Rhine in Germany, the effect of soil preparation and soil properties on species establishment on species-poor grassland had been investigated over the first three years (Schmiede et al., 2012). Here, we re-investigated the sites 13-16 years after the restoration to answer the following questions:

a) How have the target species developed on the restoration sites, and is the effect of soil preparation on species richness and composition still detectable after 13-16 years?
b) Do the restoration sites differ from the donor sites and the unrestored grassland in the close surrounding with respect to their ecological properties?
c) What is the agricultural value of the restoration sites, compared to unrestored reference grassland in the surrounding and the donor sites?
d) Which effect do soil properties, productivity, nutrient stoichiometry and hydrological characteristics of the restoration sites have on the long-term restoration success?

Materials and Methods

Study site

The study area is located approximately 30 km southwest of Frankfurt in Hesse (Germany), in the floodplain of the Northern Upper Rhine. The mean annual temperature of 11.1 °C marks the region as one of the warmest in Germany, and the mean annual precipitation is relatively low with 550 mm (HLNUG, 2022; stations Frankfurt (Main) Airport for temperature and Groß-Gerau-Wallerstädten for precipitation, 1992-2021). The fluctuating water level of the river Rhine results in both floods and droughts, with groundwater levels of up to 5 m below the surface (HLNUG, 2021). Soils are characterized by high clay contents often exceeding 50 % (Burmeier et al., 2010), which adds to the alternating soil water conditions. The specific site conditions and low-intensive haymaking supported the development of species-rich floodplain meadows of the alliances *Molinion* and *Cnidion* (habitat types 6410 and 6440 according to the EU Fauna-Flora-Habitat directive), containing a high number of rare and endangered (alluvial) grassland species (Donath et al., 2003; Hölzel, 1999). However, intensification and conversion into arable fields caused massive habitat losses in the course of the 20th century, leaving only small isolated remnants of species-rich floodplain meadows (Böger, 1991; Hölzel & Otte, 2003).

Restoration sites and measures

After a series of major floods in 1983, 150 ha of arable fields were converted to non-intensively managed, unfertilized grassland in order to re-establish species-rich floodplain meadows (Bissels et al., 2004; Böger, 1991). However, typical species hardly re-immigrated, and the re-established grassland in the study area remained rather species-poor (Schmiede et al., 2012). From 2005-2008, freshly mown plant material (seed-containing green hay sensu Kiehl et al., 2010) was gained from eight donor sites to create 20 strips (“restoration sites”) on different species-poor grassland sites. The donor sites consisted of species-rich *Molinion* or *Cnidion* meadows. Each restoration site was 120 m long and 10 m wide and divided in three segments of 40 m length, each of which had been prepared 2-7 weeks before the plant material transfer. All three segments had been mown, and then treated as following:

- *rotovated* twice,
- *ploughed* and harrowed, or
- left *untilled.*

Rotovating broke up the soil surface, while ploughing turned over the topsoil, with subsequent harrowing breaking up the new surface and levelling it (Figure 2.S1). Both treatments left a fine-grained seedbed with close to no intact vegetation, but elimination was more complete after ploughing and harrowing. However, depending on the timespan until plant material application, modest regrowth occurred on both treatments. Treatments were randomly arranged on each restoration site. Plant material transfer took place between mid-September and the end of October, when most species on the donor sites carried ripe seeds. Harvest coincided with the first cut (two donor sites, five restoration sites) or second cut (six donor sites, 15 restoration sites), depending on the mowing regime at the donor sites. A detailed description of restoration measures and sites can be found in Schmiede et al. (2012).

Vegetation sampling

Between May 10th and June 13th 2021, we investigated the vegetation on 254 plots (25 m^2). From these, 180 were located on the 20 restoration sites (nine per site, three per treatment). For nine of the 20 restoration sites, the plots had been previously studied by Schmiede et al. (2010) annually in the first three years after restoration, enabling comparison over time.

Additionally, as a reference, we placed 40 plots (two per restoration site) on the unrestored grassland surrounding all restoration sites, with a distance > 15 m to the restoration sites. Furthermore, on the eight donor sites, 34 plots were surveyed (three to five per site, depending on their size). To enable comparability with the data of Schmiede et al. (2012), species abundance was recorded using the modified Braun-Blanquet scale (van der Maarel, 1979). For data analysis, species abundance classes were transformed to percentage values following the approach of Schmiede et al. (2012). In addition to the vegetation plots, we recorded whole-site species lists for restoration and donor sites and estimated species abundances using a DAFOR scale (Norfolk Wildlife Trust, n.d.) with modifications (Table 2.S1).

Soil and biomass sampling and analysis

In April and May 2021, we gathered soil samples from each of the 254 plots. To this end, composite samples of four topsoil cores (0-10 cm) were collected using a soil corer of 2.5 cm diameter. Samples were air-dried and sieved to 2 mm. Soil pH was measured in $CaCl_2$ solution. The samples were extracted with calcium-acetate-lactate solution (CAL) for the determination of plant-available potassium (K) and phosphorus (P) (Blume et al., 2000). Total soil nitrogen (N) and carbon (C) were measured via elementary analysis (device "Unicube", co. "elementar"; DIN EN 16168, 2012; DIN EN 15936, 2012), anorganic C was calculated from the $CaCO_3$ content determined with the Scheibler method (Blume et al., 2000). The organic C content was calculated as the difference between total and anorganic C content, and the C/N ratio as the ratio between organic C and total soil N content (Kuntze et al., 1994).

For each plot, aboveground biomass was harvested in four randomly placed quadrats of 0.1 m^2 at a height of 5 cm. Sampling took place between end of May and beginning of June, shortly before the regular first grassland cut at June 8th. Most of the donor sites are cut later in summer, but were sampled at the same time for comparability. Biomass samples were merged for each plot to one composite sample, dried at 60°C for 48 hours, weighed, and milled to 0.5 mm. The acid detergent fibre (ADF), N, K and P contents were determined via Near Infrared Spectroscopy (NIRS, details see Kleinebecker et al., 2011). As measures of nutrient stoichiometry, we calculated the N/K and N/P ratios. For feeding value assessment, we calculated the crude protein content (XP) (Roth et al., 2011), the digestible energy (DE) for horses (NRC, 1999), the metabolisable energy (ME) for ruminants, and the net energy for lactation (Kirchgeßner & Kellner, 1982).

Hydrological variables

For calculation of hydrological variables, we used data from 33 groundwater wells (HLNUG, 2021) and daily water levels for 12 points of the river Rhine along the study area between January 1st, 2001 and December 31st, 2020. If data gaps for the groundwater wells were ≤ 30 days, we interpolated the groundwater levels (GWL) between adjacent time points to obtain daily groundwater water levels. The daily Rhine water levels were linearly interpolated between gauging stations Mainz, Nierstein-Oppenheim and Worms (WSV, 2021). The 45 groundwater points were used for daily Delaunay triangulation (Sinclair, 2016), including all points with an entry for the respective day. The daily groundwater level of each of the 254 plots was estimated as the inverse-distance weighted mean of the three nearest groundwater points. For each plot, we calculated three relevant hydrological predictors for species distribution (following Gattringer et al. (2019)):

- days per year with GWL > 0.7 m below ground ("Drought frequency")
- days per year with inundation height > 0.5 m ("Flood frequency")
- standard deviation of the GWL ("SD of GWL")

The location in the fossil floodplain, which is protected from flooding by a dyke, and the recent functional floodplain is often used as a hydrological predictor for ecological properties of floodplain meadows (e.g. Bissels et al., 2004; Donath et al., 2007). For our restoration sites, it was well represented by the SD of GWL. The mean was 0.72 m ± SD of 0.14 m for sites located in the functional floodplain, and 0.37 m ± 0.11 m for sites located in the fossil floodplain, respectively. Thus, we focused on the SD of GWL for further analysis, instead of the floodplain compartment.

Statistical analysis

To assess the impact of soil preparation over time, we compared the number and cover of target species (Schmiede et al., 2012, slightly modified, Table 2.1) as well as the number of species of the three soil preparation treatments for each of the first three years after restoration and for

2021 separately for the previously studied restoration sites. If an analysis of variance (ANOVA) indicated significant differences, these were identified with a Tukey honest-significant difference test (HSD) ($\alpha = 0.05$). Data were ln-transformed to meet normality and homoscedasticity, and model assumptions were checked visually using diagnostic plots (Kozak & Piepho, 2018).

To assess temporal trends of the individual target species, we calculated their occurrence frequencies in the third year after restoration and in 2021 for the previously studied restoration sites on a plot basis. For comparison, occurrence frequencies in the plant material and mean diaspore input per target species for each restoration site were calculated from the plant material data of Schmiede et al. (2010). We performed analogous frequency calculations for the corresponding unrestored reference plots of the previously studied restoration sites and for the donor site plots from the 2021 data.

We explored the temporal development of the vegetation composition on the restoration sites using non-metric multidimensional scaling (NMDS) ordination for the previously studied restoration sites for a) the first three years after restoration and b) for 2021, including the corresponding unrestored reference and donor site plots. We performed a second NMDS for all restoration sites, unrestored reference plots and donor sites. Ordinations were based on Bray-Curtis Distances, max. 100 iterations, and a random starting configuration. Three-dimensional solutions were chosen by visually checking the decrease of stress values with increasing number of dimensions, according to Leyer & Wesche (2008). To explore underlying ecological gradients, we included vectors for the number of species and target species, the proportions of plant life forms and life span groups, mean Ellenberg indicator values for light (L), temperature (T), continentality (K), moisture (F), nutrients (N) and soil reaction (R), the proportion of indicator species for alternating water levels (data from Klotz et al., 2002), as well as the soil, biomass and hydrological variables described above. The package “vegan” was used for the ordination (Oksanen et al., 2020).

We compared the different soil preparation treatments of all restoration sites with the unrestored reference grassland and the donor sites concerning soil C/N ratio, total soil N, plant available soil P and K, species and target species numbers, cover of target species, biomass yield, and energy content measures. Variables were pooled at the treatment level for the restoration sites and at the site level for the references. To this end, we performed an ANOVA, followed by a Tukey HSD test ($\alpha = 0.05$). Data were ln-transformed if diagnostic plots indicated violations against model presumptions (Kozak & Piepho, 2018).

We calculated four indicators to quantify the long-term restoration success of the restoration sites at the site level, following Kiehl et al. (2010) (Table 2.S2). These were (a) absolute transfer rate of species, (b) absolute transfer rate of target species, (c) relative transfer rate of species and (d) relative transfer rate of target species. We defined absolute and relative transfer rates for all species and for target species as the ratios between transferred and transferable species. For absolute transfer rates, species were regarded as transferable if their DAFOR abundance was R2 or higher on at least one corresponding donor site of a restoration site. For relative transfer rates, species found in the plant material from the respective restoration site (Schmiede et al., 2010) were regarded as transferable. A transferable species was regarded as transferred if recorded on a restoration site in 2021. Species from the corresponding unrestored reference plots were regarded as resident and excluded from the pool of transferable and transferred species for the respective restoration site. We opted for the calculation of both absolute and relative transfer rates as we had more data points for the absolute transfer rates ($n = 20$). However, since the relative transfer rates ($n = 15$) are based on the species composition of the plant material used for restoration, they are considered a more direct success measure. At plot level, we calculated the (e) increase in target species number and (f) increase in target species cover as the difference between the plot on the restoration site and the mean of the corresponding unrestored reference plots.

To identify factors determining the restoration success, linear regression models were used for the six success variables (a-f) separately at site level. Eleven explanatory variables were included in the model selection using the “dredge” function (R package MuMIn, Bartoń, 2020). These were the N/P and N/K ratio of the biomass, biomass yield, soil pH, plant-available P and K, soil organic C content, and the C/N ratio. Soil N content was not included due to high correlation with soil organic C ($r = 0.995$). Drought and flood frequency and the SD of GWL were included as hydrological variables. The explanatory variables were centred to a mean of 0 and scaled to a standard deviation of 1. The model with the lowest AIC that showed no multicollinearity (all variance inflation factors ≤ 2.5) was selected.

Results

Development of the restoration sites over time

The development over time can only be assessed for the previously studied restoration sites, which were restored in 2005 and 2006, so the observation period is 15-16 years here. After that time, the differences between soil preparation treatments concerning target species number and cover vanished (Figure 2.1). Compared with the first years after restoration, in the long-term, both variables remained relatively stable for the ploughed and rotovated treatments but increased for the untilled treatment. In 2021, the mean number of target species per 25 m^2 ranged from 2.2 ± 0.5 (ploughed, mean ± SE) to 3.0 ± 0.5 (rotovated), and mean target species cover ranged from 3.1 ± 0.8 (untilled) to 3.5 ± 0.9 % (rotovated). The mean number of species per plot was around 25 for all treatments. For the untilled treatment, this marked a stable trend since the third year after restoration, whereas the species number per plot decreased from around 38 to 25 species for the treatments with soil preparation. This finding was supported by the NMDS ordination of the previously studied restoration sites indicating that species composition of soil disturbance plots became more similar to the unrestored reference plots until 2021 (Figure 2.S2).

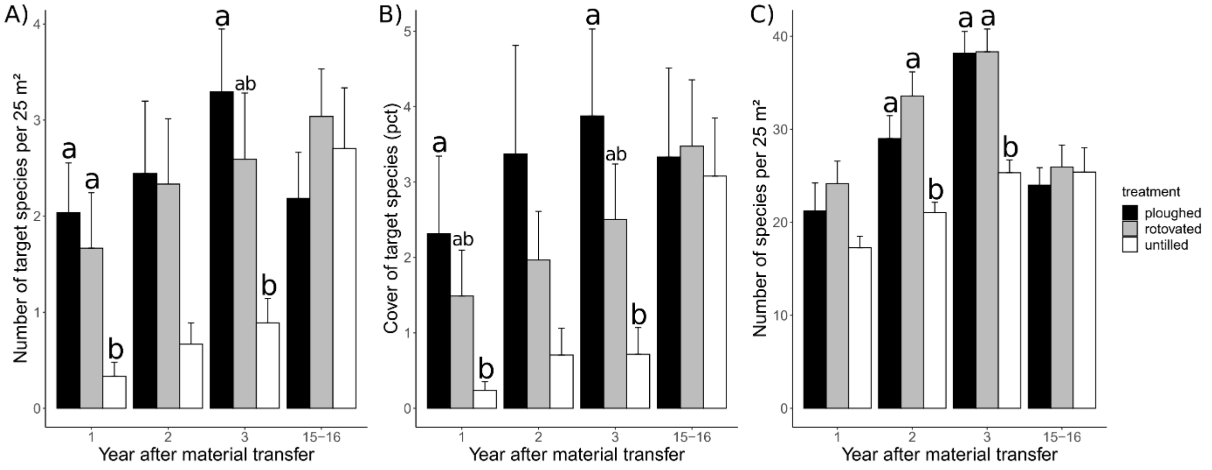

Figure 2.1: Development of the number (A) and cover (B) of target species and the number of species (C) per 25 m^2 over time after the transfer of plant material on the previously studied restoration sites for the three different treatments ploughed, rotovated and untilled (n = 9, respectively). Significant differences within years ($p < 0.05$, ln-transformed data) are indicated by different letters above the bars. Whiskers refer to the standard errors.

Out of the 46 target species, 13 showed a higher frequency at the restoration sites in 2021 compared to three years after restoration (Table 2.1). Among these, we found a range of Red List species, such as *Carex praecox*, *Galium boreale*, *Genista tinctoria*, *Iris spuria* and *Peucedanum officinale*. During the investigation period, eight target species decreased in frequency. These had been mostly recorded with low frequencies by Schmiede et al. (2010) already, such as *Bupleurum falcatum*, *Rhinanthus alectorolophus* and *Selinum carvifolia*. An exception was *Linum* *catharthicum*, which was recorded only in 1 % of the restoration plots in 2021, compared to 14 % three years after restoration. *Sanguisorba officinalis* and *Veronica maritima* remained relatively stable with a frequency of around 20 %, respectively.

Table 2.1: Development of target species over time for the previously studied restoration sites (RS) compared to corresponding unrestored reference grassland (UG) and donor sites (DS). Red List status (RL) refers to Germany (Metzing et al., 2018). * - not endangered; V – warning list; 3 – endangered; 2 – seriously endangered. For the restoration sites, frequencies are given for the third year after restoration and for 2021. The trends are only given for species with a frequency > 3 % in at least one year. If the change is ≤ 20 % of the 3rd year value, the trend is regarded as stable. Frequencies for plant material (PM) and the mean diaspore input (MDI, units per m^2) refer to plant material samples (n = 9) taken by Schmiede et al. (2010).

			Frequency (%)					
Target species	**RL**	**Trend on RS**	**RS (3rd year)**	**RS (2021)**	**UG**	**DS**	**PM**	**MDI**
Increased frequency								
Arabis hirsuta	V	↗	0	17	11	15	0	0
Bromus erectus	*	↗	0	6	0	32	22	6
Carex praecox	V	↗	2	15	6	12	78	12
Galium boreale	V	↗	9	17	0	15	78	225
Genista tinctoria	V	↗	2	11	0	41	22	9
Inula britannica	V	↗	9	11	0	6	89	1636
Inula salicina	V	↗	17	26	11	53	100	890
Iris spuria	2	↗	0	21	0	12	33	9
Peucedanum officinale	3	↗	9	17	0	50	56	6
Pimpinella saxifraga	*	↗	4	5	0	6	33	6
Scutellaria hastifolia	2	↗	2	4	0	3	33	1
Viola pumila	2	↗	0	5	0	6	56	15
Viola stagnina	2	↗	1	4	0	12	11	5
Reduced frequency								
Arabis nemorensis	2	↘	47	31	11	12	89	1294
Bupleurum falcatum	V	↘	4	0	0	3	0	0
Dipsacus laciniatus	*	↘	6	0	0	0	11	0
Linum catharticum	*	↘	14	1	6	12	78	39
Rhinanthus alectorolophus	*	↘	5	0	0	6	0	0
Selinum carvifolia	V	↘	6	2	11	18	44	16
Senecio aquaticus	V	↘	5	2	0	0	0	0
Silaum silaus	V	↘	7	5	6	21	33	4
Stable frequency								
Sanguisorba officinalis	V	↔	20	19	0	62	67	2

			Frequency (%)					
Target species	**RL**	**Trend on RS**	**RS (3rd year)**	**RS (2021)**	**UG**	**DS**	**PM**	**MDI**
Thalictrum flavum	V	↔	4	4	6	9	33	2
Valeriana pratensis.	*	↔	15	15	11	21	11	1
Veronica maritima	V	↔	19	19	0	6	56	89
No establishment								
Allium angulosum	3	-	0	0	0	15	78	139
Betonica officinalis	V	-	0	1	0	12	0	0
Bromus racemosus	3	-	0	2	11	12	0	0
Carex panicea	V	-	0	0	0	18	22	1
Carex tomentosa	3	-	1	0	0	29	89	4
Cirsium tuberosum	3	-	2	1	6	15	0	0
Gentiana pneumonanthe	2	-	0	0	0	3	0	0
Hippocrepis comosa	V	-	1	0	0	6	0	0
Iris sibirica	3	-	0	1	0	12	11	0
Juncus alpinoarticulatus	V	-	0	0	0	0	0	0
Lathyrus palustris	3	-	0	0	0	3	0	0
Lotus maritimus	3	-	1	0	0	9	22	1
Lotus tenuis	V	-	2	0	0	3	33	3
Melampyrum cristatum	3	-	2	0	0	21	0	0
Molinia caerulea	*	-	2	0	0	24	56	40
Potentilla erecta	*	-	2	0	0	12	22	1
Sanguisorba minor	*	-	1	0	0	6	0	0
Selinum dubium	2	-	0	0	0	3	0	0
Serratula tinctoria	3	-	1	1	0	32	56	10
Succisa pratensis	V	-	1	0	0	32	11	0
Viola elatior	2	-	0	0	0	6	44	1

Ecological comparison between restoration sites and references

The NMDS of all restoration sites and the references for 2021 revealed that the donor sites were separated from the unrestored reference grassland and the restoration sites (Figure 2.2). While there was a wide overlap between the latter two groups, the centroid of the unrestored reference grassland was separated from the centroids of the restoration soil treatments, which were all slightly shifted towards the donor sites. The donor sites were characterized by higher target species and species numbers, energy contents, Ellenberg R values, and drought frequency compared to the other groups. Both the restored and unrestored sites were characterized by higher productivity levels, indicated by increased Ellenberg N values and biomass yields compared with the donor sites.

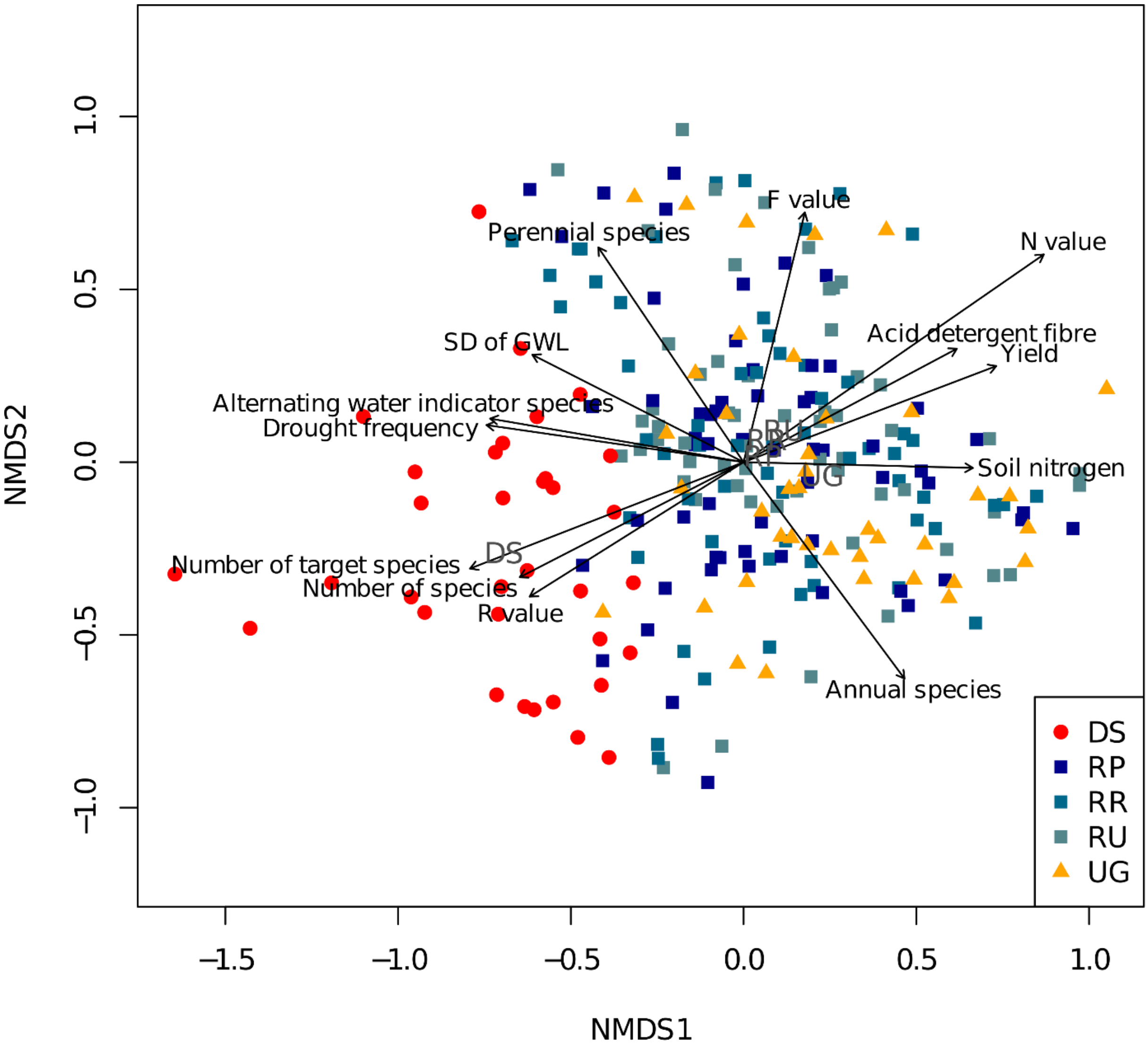

Figure 2.2: NMDS of the vegetation plots for all restoration sites, the unrestored reference grassland and the donor sites in 2021 (axis 1 and 2 of the three-dimensional solution are shown). Final stress: 16.9. Plots are grouped by donor sites (DS), unrestored reference grassland (UG), and restoration sites with the treatments ploughed (RP), rotovated (RR) and untilled (RU). The group labels are located at the centroids of the groups. Vectors with $r^2 > 0.3$ are displayed. For better readability, the cover of target species, the metabolisable energy (high correlation with number of species and target species) were removed despite $r^2 > 0.3$.

Concerning soil nutrient status, the restoration sites and the unrestored reference grassland were very similar (Figure 2.3). Their C/N ratio averaged at 11.0 ± 0.1 (± SE), compared to 11.9 ± 0.3 for the donor sites. No significant differences between the groups were found for total nitrogen, plant-available P and K contents. However, soil nutrient contents of the donor sites were lower than those of the restoration sites and unrestored reference plots. Especially the low and very narrow plant-available P content of the donor sites (0.9 ± 0.1 %) was noticeable.

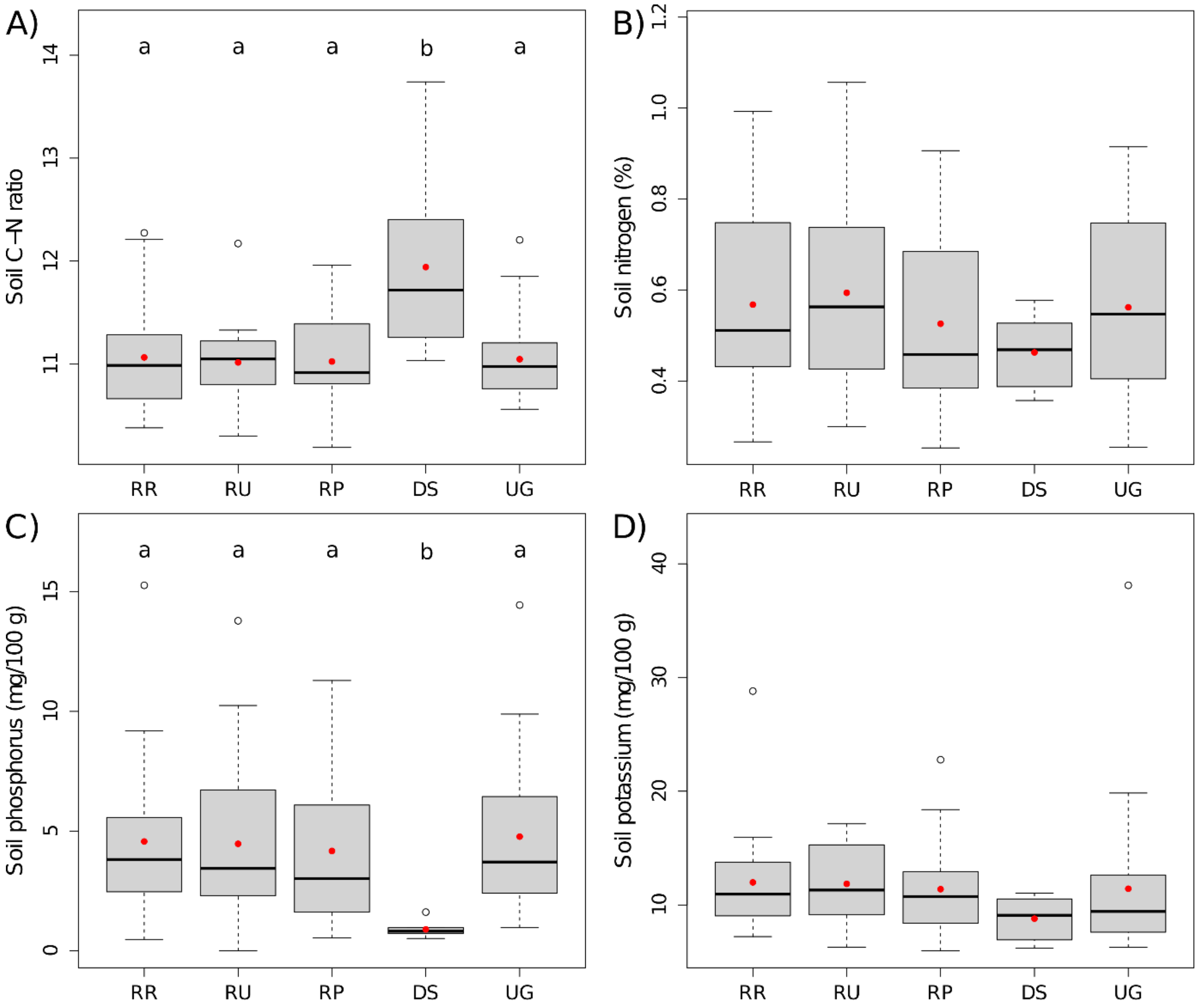

Figure 2.3: Box-whisker plots of the soil C/N ratio (A), total nitrogen (%) (B), plant-available P (mg/100 g) (C) and plant-available K (mg/100 g) (D) in 2021 on the different site categories - donor sites (DS, n = 8), all restoration sites with treatments ploughed (RP), rotovated (RR) and untilled (RU), and unrestored reference grassland (UG) (n = 20, respectively). Plot data were averaged on the treatment level or, in case of DS and UG, on the site level. Red dots display the mean values. Significant differences ($p < 0.05$) are indicated by different letters above the boxes (testing on ln-transformed data for soil P and soil K).

In 2021, over all restoration sites, the number of target species per plot was similar for all soil treatments with an average of 1.9 ± 0.3 (Figure 2.4A) and significantly higher than for the unrestored reference grassland (0.7 ± 0.2), but significantly lower than for the donor sites (7.0 ± 1.4). Although not significant, mean cover of target species was higher on the restoration sites (2.1 ± 0.4 %) than on the unrestored reference grassland (1.3 ± 0.6 %) (Figure 2.4B). For the donor sites, however, target species cover was significantly and markedly higher (mean = 19.7 ± 5.0 %). The same held true for the number of recorded plant species (Figure 2.4C).

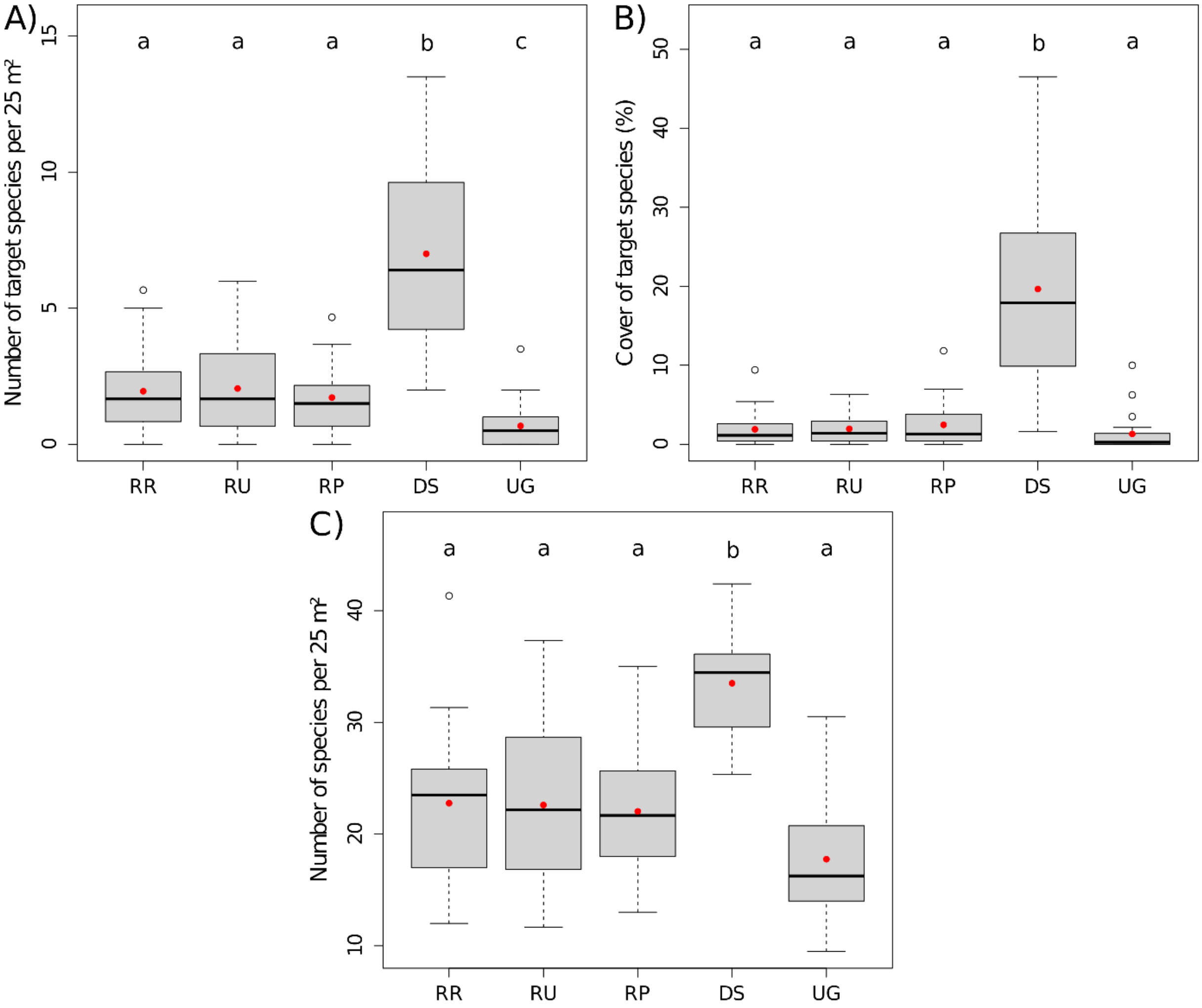

Figure 2.4: Box-whisker plots of the number of target species per plot (A), the cover of target species (%) (B) and the number of species per 25 m² plot (C) in 2021 on the different site categories - donor sites (DS, n = 8), all restoration sites with treatments ploughed (RP), rotovated (RR) and untilled (RU), and unrestored reference grassland (UG) (n = 20, respectively). Plot data were averaged on the treatment level or, in case of DS and UG, on the site level. Red dots display the mean values. Significant differences ($p < 0.05$) are indicated by different letters above the boxes (testing on ln-transformed data for number and cover of target species).

Feeding value of the grassland stands

The biomass yield levels of the restoration sites (407 ± 26 g/m²) and the unrestored reference grassland (421 ± 36 g/m²) did not differ but both were significantly higher compared to the donor sites, which had an average yield of 239 ± 29 g/m² (Figure 2.5A). The energy content variables for cattle and horses were similar between restoration sites and the unrestored reference grassland, with those of the donor sites being 4-5 % higher (Figure 2.5B, C and D).

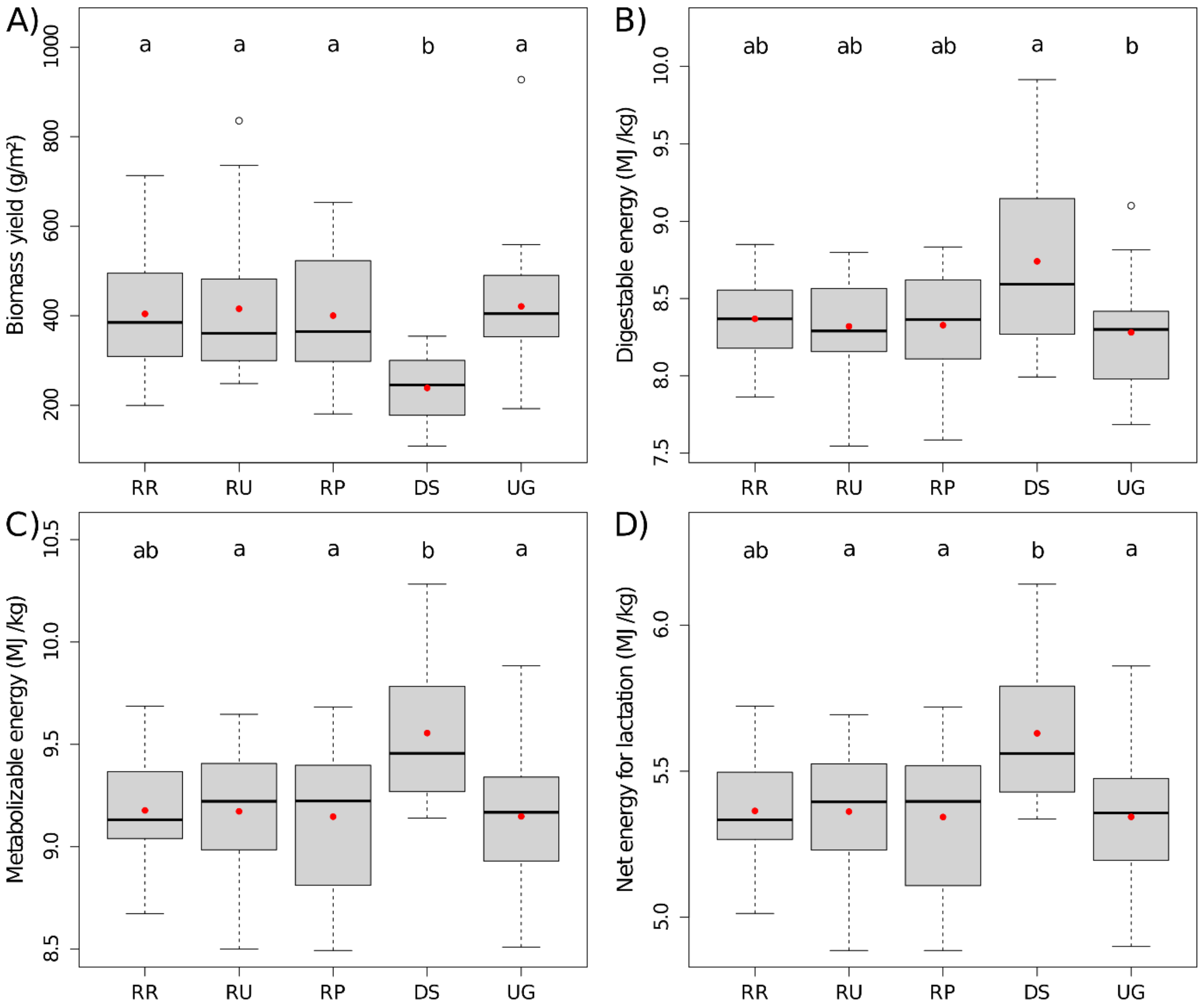

Figure 2.5: Box-whisker plots of the biomass yield (g/m²) (A), the digestible energy for horses (MJ/kg) (B), the metabolisable energy for ruminants (MJ/kg) (C), and the net energy for lactation (MJ/kg) (D) (all referring to dry matter) in 2021 on the different site categories - donor sites (DS, n = 8), all restoration sites with treatments ploughed (RP), rotovated (RR) and untilled (RU), and unrestored reference grassland (UG) (n = 20, respectively). Plot data were averaged on the treatment level or, in case of DS and UG, on the site level. Red dots display the mean values. Significant differences ($p < 0.05$) are indicated by different letters above the boxes (testing on ln-transformed data for biomass yield).

Drivers of restoration success

Absolute transfer rates of both all species and target species averaged at 40.1 ± 3.9 and 36.4 ± 6.2 %, respectively (Table 2.S2). The corresponding relative transfer rates were 24.9 ± 1.6 and 34.7 ± 3.7 %. Higher biomass yield was generally associated with lower numbers of target species and reduced absolute transfer rates of species and target species (Table 2.2). The C/N ratio was positively associated with both the number and the cover of target species. Out of the hydrological variables, higher flood frequency tended to reduce restoration success, while higher drought frequency and variation of the groundwater level tended to have positive effects. The R^2 of the selected models ranged from 36 % to 65 %, except for the relative transfer rate of species, which could not be explained (R^2 = 1 %).

Table 2.2: Overview of the regression models selected by AIC criterion for the ecological restoration success variables on the site level. TR – transfer rate. Rows represent the estimates for the different explanatory variables included in the selected models – the biomass yield, the C/N ratio, plant-available P content and pH of the soil, the SD of the groundwater level, the flood and drought frequency (all standardized to mean = 0 and SD = 1). Variables with a dot were not selected in the respective model. Significance levels are given as following: *** - $p \leq 0.001$, ** - $p \leq 0.01$, * - $p \leq 0.05$. n – number of observations, R^2 - adjusted R^2 of the model, AIC – Akaike information criterion, λ - value of λ for the Box-Cox transformation of the response variable.

	Absolute TR target species (%)	**Absolute TR species (%)**	**Relative TR target species (%)**	**Relative TR species (%)**	**Increase in target species number per plot**	**Increase in target species cover (%)**
Intercept	5.578***	40.111***	21.993**	24.952***	1.231***	28.588***
Biomass yield	-1.564***	-9.817*	.	.	-0.591*	.
Soil C/N ratio	.	.	.	.	1.039***	4.657*
Soil P	.	5.968	.	.	.	.
Soil pH	.	.	15.183	.	.	.
SD of GWL	.	.	.	.	.	4.925*
Flood frequency	-0.998*	-4.351	.	-1.784	-0.567*	-2.682
Drought frequency	.	.	13.310*	.	.	.
n	20	20	15	15	20	20
R^2	0.65	0.39	0.36	0.01	0.60	0.42
AIC	78.2	166.4	120.2	100.2	60.4	145.9
λ	0.5	1	1	1	1	1.5

Discussion

Vegetation development over time

We found no effect of soil preparation on vegetation development and target species establishment 13 to 16 years after restoration. This is surprising, as one of the main findings of Schmiede et al. (2012) was that soil disturbance, especially ploughing, enabled better (target) species establishment due to suppression of the existing grassland vegetation. This is a common observation among different grassland types, so that soil preparation prior to diaspore introduction in species-poor grassland is often recommended (Kiehl et al., 2010). However, studies deriving such advice from their findings mostly have short observation timeframes and to the best of our knowledge do not exceed eight years (Bischoff et al., 2018; Durbecq et al., 2021; Edwards et al., 2007). In line with our findings, recent studies on floodplain meadow restoration by Harvolk-Schöning et al. (2020) and Heilscher (2020) indicate that the positive effect of soil preparation on the number and cover of introduced species diminishes in the long run.

Initially, soil disturbance creates micro-niches for germination and establishment of species from the plant material (Harvolk-Schöning et al., 2020), but also activates the soil seed bank (Ludewig et al., 2021; Schmiede et al., 2012). In the short term, this leads to promotion of ruderal species (Klaus et al., 2018). Accordingly, in our experiment, ruderal species such as *Cirsium arvense*, *Galium aparine* or *Lactuca serriola* emerged in high frequencies over the first three years after restoration, but receded in the long run. In contrast, some target species such as *Inula britannica* or *Carex praecox* emerged later or developed more slowly. This was presumably due to competition with the resident vegetation, but these species established in the long run even without tillage.

Across all treatments, target species that were already present three years after restoration mostly remained stable or increased in frequency until 2021. This is in accordance with the stable target species number on plots with soil disturbance and the observed increase for the untilled treatment. An especially encouraging case is *Iris spuria*, which was not detected by Schmiede et al. (2012) in the first three years after restoration, but was detected in considerable amounts on two restoration sites in 2021. The hard seed coat of this species can delay germination, so that establishment happens only after longer time periods (Hölzel & Otte, 2004b). Harvolk-Schöning et al. (2020) observed a similar pattern for *Iris spuria* on former arable fields. Our results clearly show that in the longer term, the establishment of this highly endangered species is possible on grasslands lacking typical floodplain meadow species.

Many target species were not successfully established, some of them despite frequent occurrence on the donor sites. For example, *Succisa pratensis* was barely captured in the plant material, which may be due to asynchronous fruit ripening with only a small proportion of ripe seeds when the plant material was harvested, as this species has a long flowering and seed shedding period (Adams, 1955). However, after-ripening of seeds may lead to increased germination even when they are harvested in an unripe state, as was shown for the non-native *L. polyphyllus* in mountain grasslands (Klinger et al., 2020). Diaspores of *Allium angulosum*, *Selinum carvifolia* and *Serratula tinctoria* were captured in considerable amounts (in ≥ 44 % of plant material samples and with ≥ 10 diaspores per m^2 on average, respectively), but established poorly or not at all, with an occurrence frequency of 6 % at maximum on the previously studied restoration sites over the whole observation period. This matches with observations by Harvolk-Schöning et al. (2020), and could be a consequence of specific germination requirements, e.g. characteristic temperature regimes (Hölzel & Otte, 2004a; Wagner et al., 2021).

Ecological comparison of restoration sites, unrestored reference grassland and donor sites

Our findings on the nutrient levels for the grassland sites overall matched those of former studies in the region (Donath et al., 2007; Donath et al., 2015; Schmiede et al., 2012). Grasslands of high nature conservation value, often used as donor sites, consistently had much lower plant-available P contents and moderately lower plant-available K contents than species-poor grassland sites often chosen for restoration. For the N contents, no such pattern had been found in those studies. In our study, the tendency to increased N contents of the restoration sites and the untreated reference grasslands compared with the donor sites is probably due to seven restoration sites with high organic C contents of 8.6 ± 0.5 % (mean ± standard error; vs. 4.9 ± 0.3 % for the other 13 restoration sites). The higher average C/N ratios of the donor sites are mainly driven by two poor *Molinion* sites with very wide ratios of 12.9 and 13.7, respectively.

A range of rare and endangered plant species of floodplain meadows, many of which are listed in the Red Lists of Germany and Hesse, were successfully established on the restoration sites. However, our results confirm that the ecological restoration of grassland is challenging, even if the sward is disturbed prior to diaspore introduction (Hansen et al., 2022; Harvolk-Schöning et al., 2020; Kiehl et al., 2010). Thirteen to sixteen years after restoration, the vegetation composition of the restored plots was similar to the unrestored reference grassland plots, with only slight changes towards the composition of the donor sites. Nevertheless, the number of target species was significantly higher for restoration sites and also their cover increased, compared with the unrestored reference.

Feeding value of the site categories

Different restoration measures affected neither the yield nor the energy content of the aboveground biomass. While a change in yield was not expected, a more diverse species composition with a higher proportion of forbs can be associated with higher energy contents of the biomass in floodplain meadows (Donath et al., 2004). The similar biomass energy contents of restored and unrestored reference grasslands can be explained by the marginal effects of restoration measures on the overall vegetation composition.

The yield levels of the restored and unrestored grasslands in our study system are mostly within the previously observed range of non-intensively managed grasslands of wet and mesotrophic sites (Donath et al., 2015; Tallowin & Jefferson, 1999). With dry matter yields of up to 705 g/m², some sites exceeded the levels normally reached without fertilization (Tallowin & Jefferson, 1999). Under these conditions and with regard to the current subsidy policy (EU area bonus and conservation contracts), haymaking is economically viable for the regional farmers. For lactating cows, the hay may be at best recommended as basic feed, as the net energy for lactation of 5.4 ± 0.2 MJ/kg dry matter (mean ± SD) would require supplementation with high-energy compounds (Donath et al., 2004; Donath et al., 2021; Schumacher, 2016). The metabolisable energy contents of 9.2 ± 0.3 MJ/kg dry matter indicate suitability as complete feed for non-lactating cows (DLG, 2009; Donath et al., 2004) and empty ewes or ewes in early pregnancy, as well as for integration in compound feed rations for calves (LfL, 2021). Practically, most of the hay harvested in the region is used for leisure horses. The hay from our restoration sites and their surroundings is suitable for this with regard to the observed digestible energy levels of 8.3 ± 0.3 MJ/kg dry matter (Donath et al., 2004; NRC, 1999).

Slightly higher energy contents of the biomass from highly species-diverse donor sites indicate that an increase in species diversity does not preclude the integration of species-rich swards into feeding rations (Donath et al., 2004; Tallowin & Jefferson, 1999). However, yield of the donor sites is on average 40 % lower compared to the restoration sites, which makes it difficult for farmers to operate profitably. Thus, agri-environmental schemes obviously remain an important pre-requisite in the conservation of species-rich grasslands of high-nature value (Donath et al., 2021).

Drivers of restoration success

The transfer rates we observed were within the typical range for plant material transfer on species-poor grassland, but lower than on former arable fields (Kiehl et al., 2010). This holds true for both target species as well as total species numbers. While biomass yield and flood frequency had negative impacts, wider C/N ratios positively affected restoration success. These three predictors were identified as significant for at least two success variables.

Biomass yield levels are the result of complex interactions of biotic and abiotic factors (Doyle, 1982), with different nutrients being decisive in different locations and years (Fay et al., 2015). Beside generally relatively fertile soils in floodplains, we suspect that productivity in our restoration sites is partly increased by remnants of former fertilization, which may be the reason for the very high yield levels of some of the sites. Due to the dominance of tall and highly productive grasses under fertile conditions (Honsova et al., 2007), high productivity reduced the suitability for the establishment of species-rich floodplain meadows.

Regular flooding events lead to nutrient deposition in close proximity to the river channel (Klaus et al., 2011; Poulsen et al., 2014) and increase the productivity of floodplain meadows by higher soil nutrient levels (Beltman et al., 2007). Apart from this, higher water availability increases mineralization and nutrient supply, which leads to highly variable biomass yield between years (Mathar et al., 2015), but also between sites (cf. Jakrlová, 1999). In our study, the positive relationship between flood frequency and biomass yield ($r = 0.35$, Figure 2.S3) could result from a mixture of the fertilizing and the mineralizing effect of frequent flooding events. This may explain the identification of flood frequency as negatively affecting restoration success along with the biomass yield observed in 2021. Another reason for the adverse effect of flood frequency on restoration success might be that long flooding of seedlings emerged from transferred plant material impedes survival (Bao et al., 2018; Gattringer et al., 2018).

Increased soil C/N ratios were significantly associated with increases in target species number and cover. The C/N ratio in the soil as an indicator of N availability could be another long-term determinant of productivity. However, the positive correlation between C/N ratio and yield ($r = 0.30$) does not support this. Higher C/N ratios, although not reducing productivity, could facilitate the establishment of typical floodplain meadow species by reducing competition with generalist grassland species adapted to high and continuous N availability. Accordingly, adverse effects of soil nitrogen on target species establishment were observed in the floodplain of the river Elbe (Dullau et al., 2021).

While Schmiede et al. (2012) identified plant available P content in the soil to negatively affect target species numbers in our study system, our resurvey cannot confirm this for the long term. Considering an extended set of factors and sites, the restoration sites rich in organic C, which had not been covered by the study of Schmiede et al. (2012), were among the more productive ones, so that the overall effect of biomass yield might have masked the effect of soil P.

Conclusions

In our study, we found no long-term effect of soil preparation on vegetation development and target species establishment across a large dataset. This indicates that the positive effect of soil preparation on the number and cover of target species, which is regularly reported in short-term studies, diminishes over time, while the effects of local site conditions become more important. Therefore, soil preparation prior to seed introduction may not be necessary in floodplain meadow restoration. To increase restoration success, the productivity of restoration sites, soil C/N ratios, and flooding frequency should fit to the respective restoration goals. For practitioners, choosing restoration sites with productivity levels not greatly exceeding those of the donor sites may be most feasible. If restoration sites are too productive, management schemes that actively reduce site productivity are recommended.

Concerning biomass characteristics, we showed that despite considerable differences in yield, even restoration sites with low productivity provide biomass of sufficient amount and feeding value. Thus, the integration of restored grasslands in local farming systems is possible and can ensure long-term management and thus stability of these ecosystems. Furthermore, one-time introduction of target species showed only limited success. Thus, additional plant material transfer or manual seeding of target species is probably necessary. Further studies should investigate the potential of such supplementary measures. Overall, we strongly recommend long-term monitoring of restoration projects in other regions and grassland types, as factors determining restoration success may become evident only after longer time periods.

Author contributions

TWD, TK and SH conceived of the research idea and designed the study. LS gathered and analysed the data with the help of YK and SH, and wrote the first draft of the manuscript. All authors contributed to revise the first draft of the manuscript and gave final approval for publication.

Acknowledgements

We thank the German Federal Environmental Foundation for funding the study. We express our gratitude to J. Scholz vom Hofe for his exertion in soil and biomass sampling and sample processing, to J. Höhl for the lab analyses, and to S. Flecken for her input on the feeding value aspects of this manuscript. A thank you goes to M. Harnisch from the city of Riedstadt and to R. Baumgärtel from the forestry administration Groß-Gerau for their professional and administrative help at the Northern Upper Rhine, as well as to the local farmers who patiently supported our investigations. We are grateful to N. Hölzel from the University of Münster for his ideas on the sampling design and the interpretation of results, and to M. Hahn and K. Willkomm for their help during field work.

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Supplementary materials

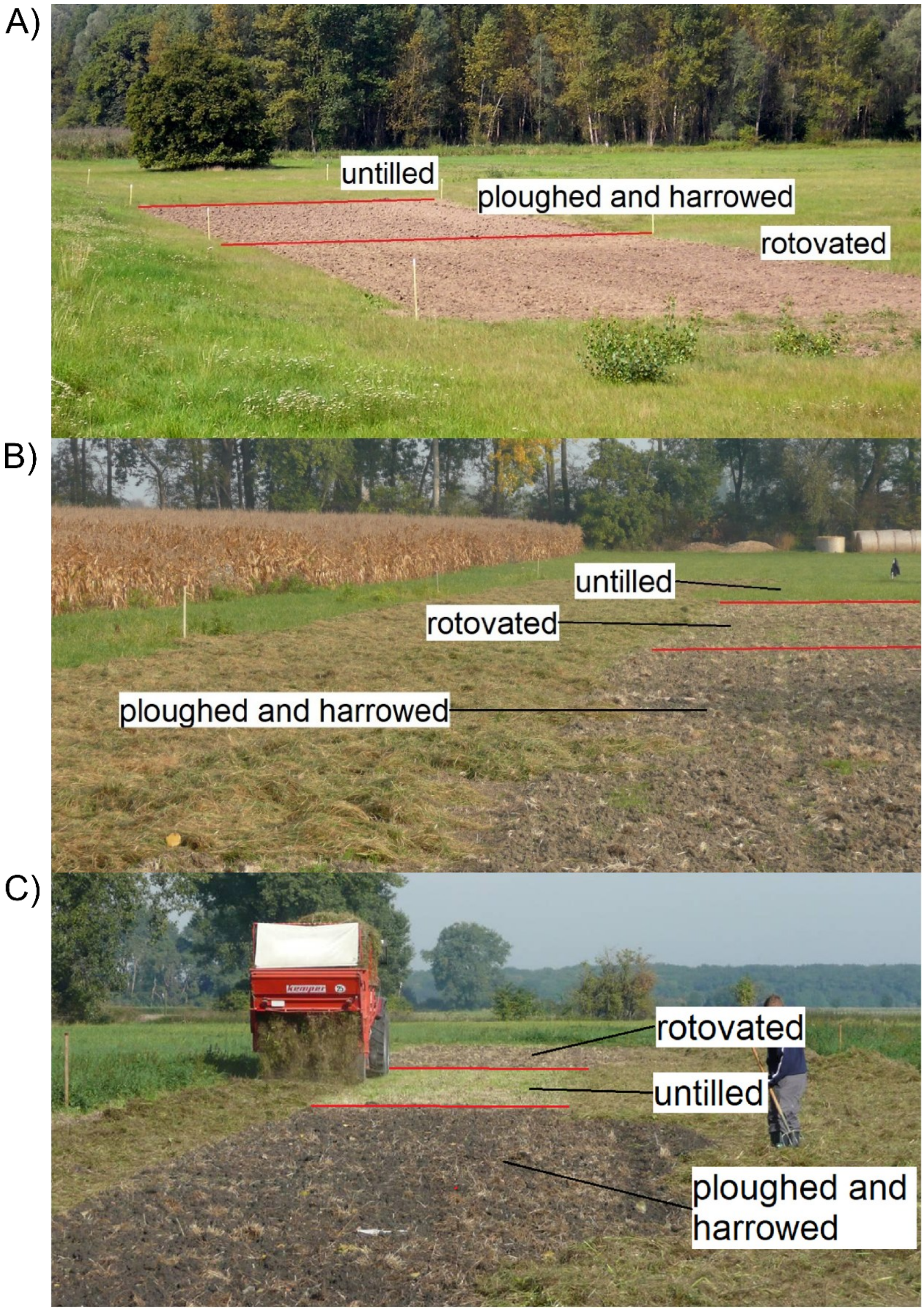


Figure 2.S1: The different soil preparation treatments (*ploughed* and harrowed, *untilled*, *rotovated* twice) on three restoration sites: (A) Prior to plant material application, (B) and (C) with plant material already partly applied. In the *ploughed* and harrowed treatment, the soil surface was broken up and levelled after turning over the topsoil, so it looks similar to the *rotovated* treatment. Red lines indicate the borders between the treatments. Photos: Matthias Harnisch, City of Riedstadt.

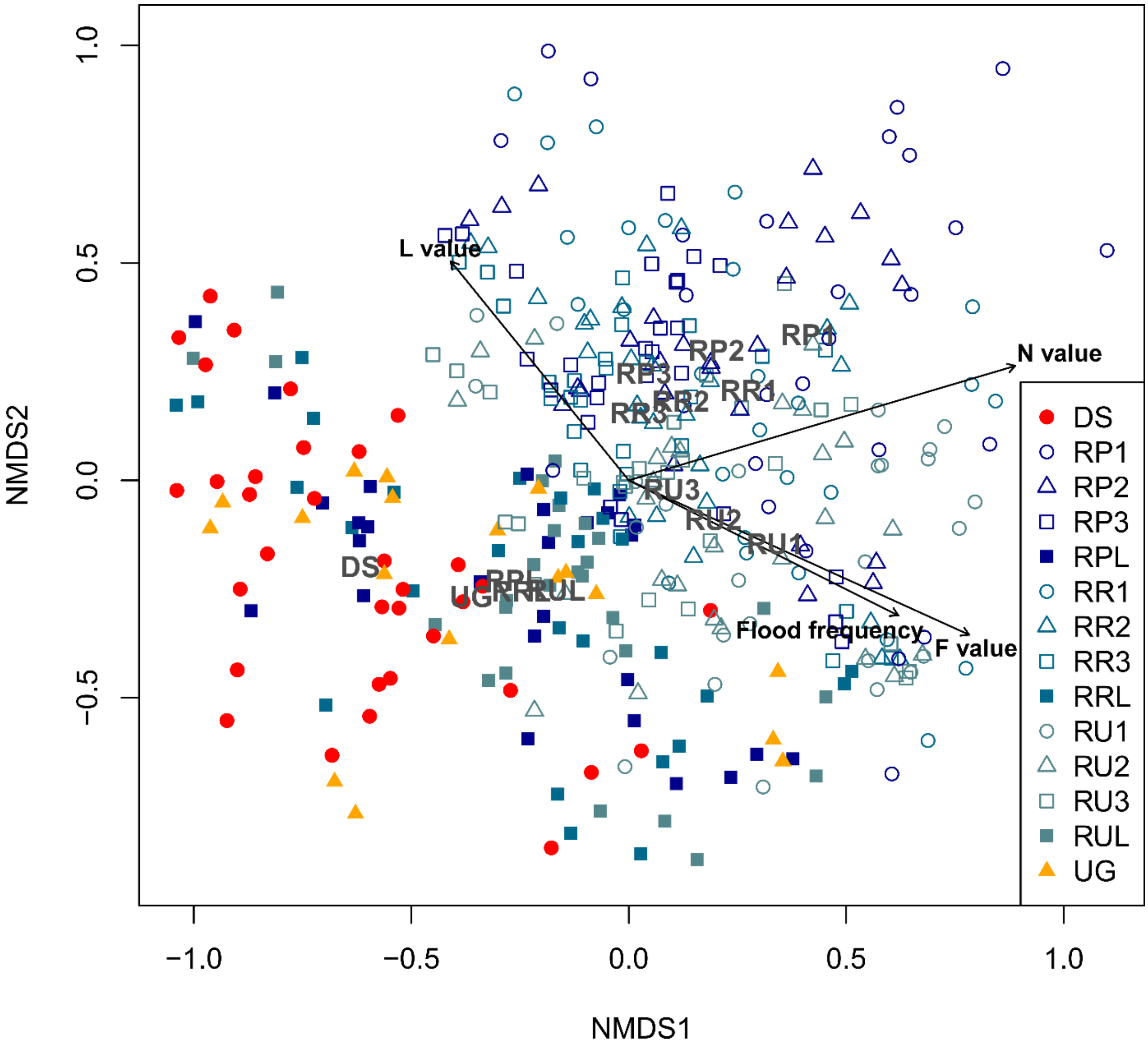
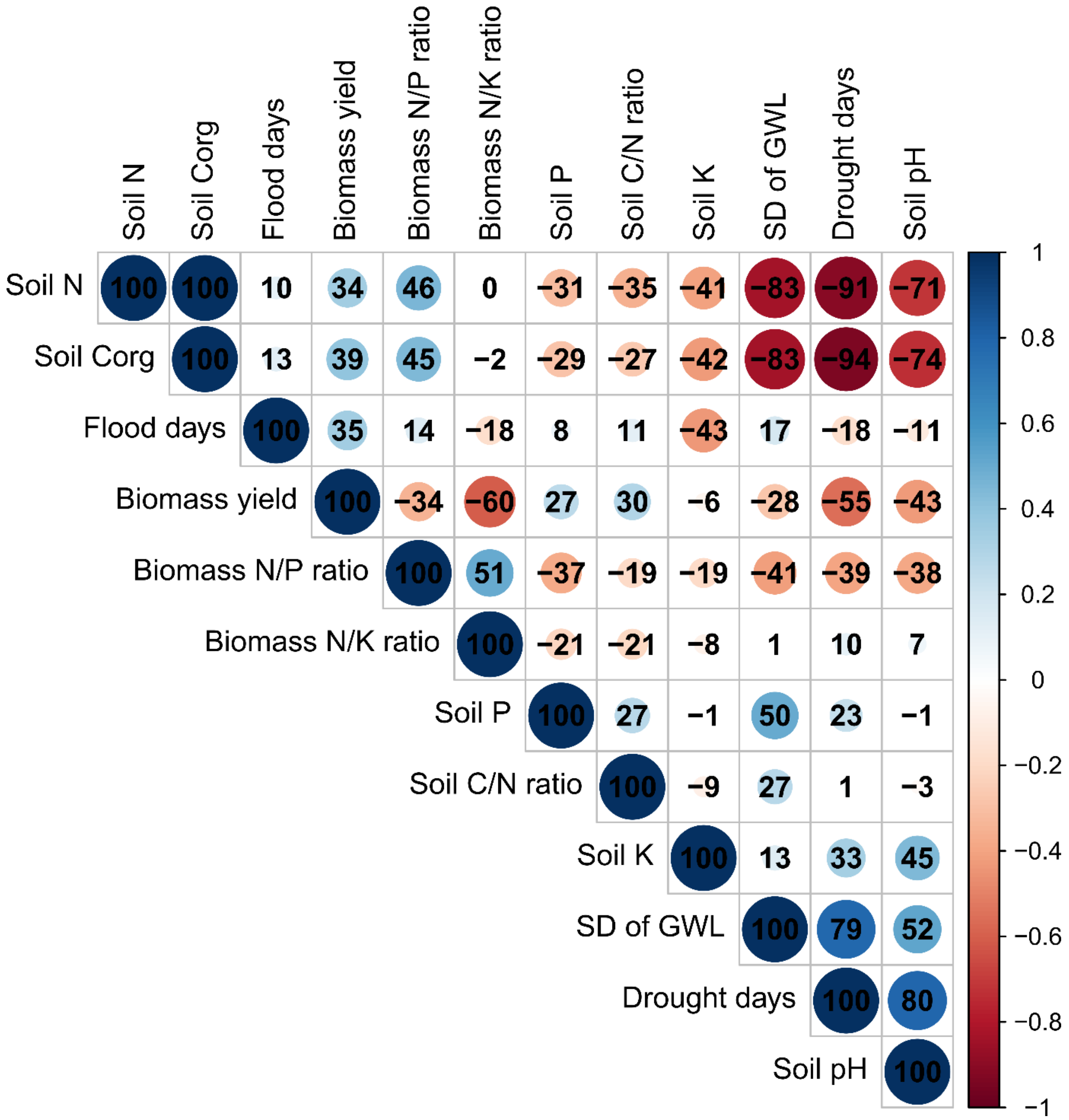


Figure 2.S2: NMDS plot showing the vegetation development over time for the treatments of the previously studied restoration sites on plot basis. Data for corresponding donor sites and unrestored reference plots are included. Axis 1 vs. axis 2 of a three-dimensional solution with a final stress of 18.3 is shown. Plots are grouped by donor sites (DS), unrestored reference grassland (UG), and restoration sites with the treatments ploughed (RP), rotovated (RR) and untilled (RU). The grouping for the restoration sites additionally comprises the year after plant material transfer (1 to 3 and L (long-term, i.e. 15-16 years)). The group labels are located at the centroids of the groups. Vectors with $r^2 > 0.3$ are displayed.



	Soil N	Soil Corg	Flood days	Biomass yield	Biomass N/P ratio	Biomass N/K ratio	Soil P	Soil C/N ratio	Soil K	SD of GWL	Drought days	Soil pH
Soil N	100	100	10	34	46	0	−31	−35	−41	−83	−91	−71
Soil Corg		100	13	39	45	−2	−29	−27	−42	−83	−94	−74
Flood days			100	35	14	−18	8	11	−43	17	−18	−11
Biomass yield				100	−34	−60	27	30	−6	−28	−55	−43
Biomass N/P ratio					100	51	−37	−19	−19	−41	−39	−38
Biomass N/K ratio						100	−21	−21	−8	1	10	7
Soil P							100	27	−1	50	23	−1
Soil C/N ratio								100	−9	27	1	−3
Soil K									100	13	33	45
SD of GWL										100	79	52
Drought days											100	80
Soil pH												100

Figure 2.S3: Pearson correlation matrix of the factors for the model selection for all restoration sites in 2021 in %. Soil N was excluded from the selection due to the high correlation with Soil C_{org}.

Table 2.S1: Classes of the modified DAFOR scale for the whole-site species lists.

Abundance		**Cover** (%)
D	Dominant	50-100
A	Abundant	25-50
F	Frequent	15-25
O	Occasional	5-15
R2	rare; occurring regularly over the site with many individuals	<5
R1	rare; occurring in few places or with few individuals	<5

Table 2.S2: Mean, standard deviation (SD), maximum (max), minimum (min) and sample size (number of sites, n) for the calculated variables of restoration success in 2021. TR: transfer rate.

	Absolute TR target species (%)	**Absolute TR species (%)**	**Relative TR target species (%)**	**Relative TR species (%)**	**Increase in target species number per plot**	**Increase in target species cover (%)**
Mean	36	40	35	25	1.2	0.8
SD	28	17	14	6	1.5	2.6
max	100	71	53	36	4.2	5.9
min	0	6	0	16	-1.7	-7.4
n	20	20	15	15	20	20

Chapter 3: Grassland Restoration Practice in Central Europe: Drivers of success across a broad moisture gradient

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2025, *Restoration Ecology*, 33(7), e70106. doi: 10.1111/rec.70106

Abstract

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 restored 3-18 years ago via plant material transfer with composition of their donor sites. Spanning diverse moisture conditions, sites were located in Germany and Luxembourg. We also analysed establishment of habitat-typical and endangered species. 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 creation of raw soils at several sites before plant material application. While raw soils generally favoured 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 generally 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 provide guidance on addressing this complex challenge in the coming decades.

Keywords

abiotic conditions, green hay transfer, monitoring, plant material transfer, Red List species, raw soil, 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 aesthetic 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).

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, Castro Campos, et al., 2023). 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, Klinger, et al. 2023). 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 (De Vitis et al., 2022; Scotton et al., 2012).

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, Klinger, et al. 2023). 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 standardised 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, Castro Campos, et al., 2023).

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 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, Castro Campos, et al., 2023), 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: site 4 (Storm et al., 2022), 5, and 6 (both from Storm et al. (2016); see Table 3.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 1991-2020 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 3.S1). In total, we investigated 37 donor sites (size of 0.07 to 6.82 ha) and 41 recipient sites (0.02 to 11.9 ha) of plant material transfer. Individual donor sites were used to transfer plant material to 1–4 recipient sites, and material from 1-4 donor sites was applied to individual recipient sites. The measures had been carried out 3-18 years before our investigation. We categorised the recipient sites based on the respective donor sites, defining four target grassland types, i.e., *dry* grasslands, *mesic* grasslands, *alluvial* grasslands with alternating water conditions, and *wet* grasslands (section “Definition of target grassland types”).

Before restoration, most recipient sites had been grasslands, arable fields (with crop production abandoned up to one season before restoration), or spruce plantations (see proportions in Figure 3.1, Table 3.S1). Extant vegetation was reduced by combinations of mowing, mulching (cutting without removal of the clippings), or clearing, and soil preparation measures (ploughing, rotovating, 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 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.

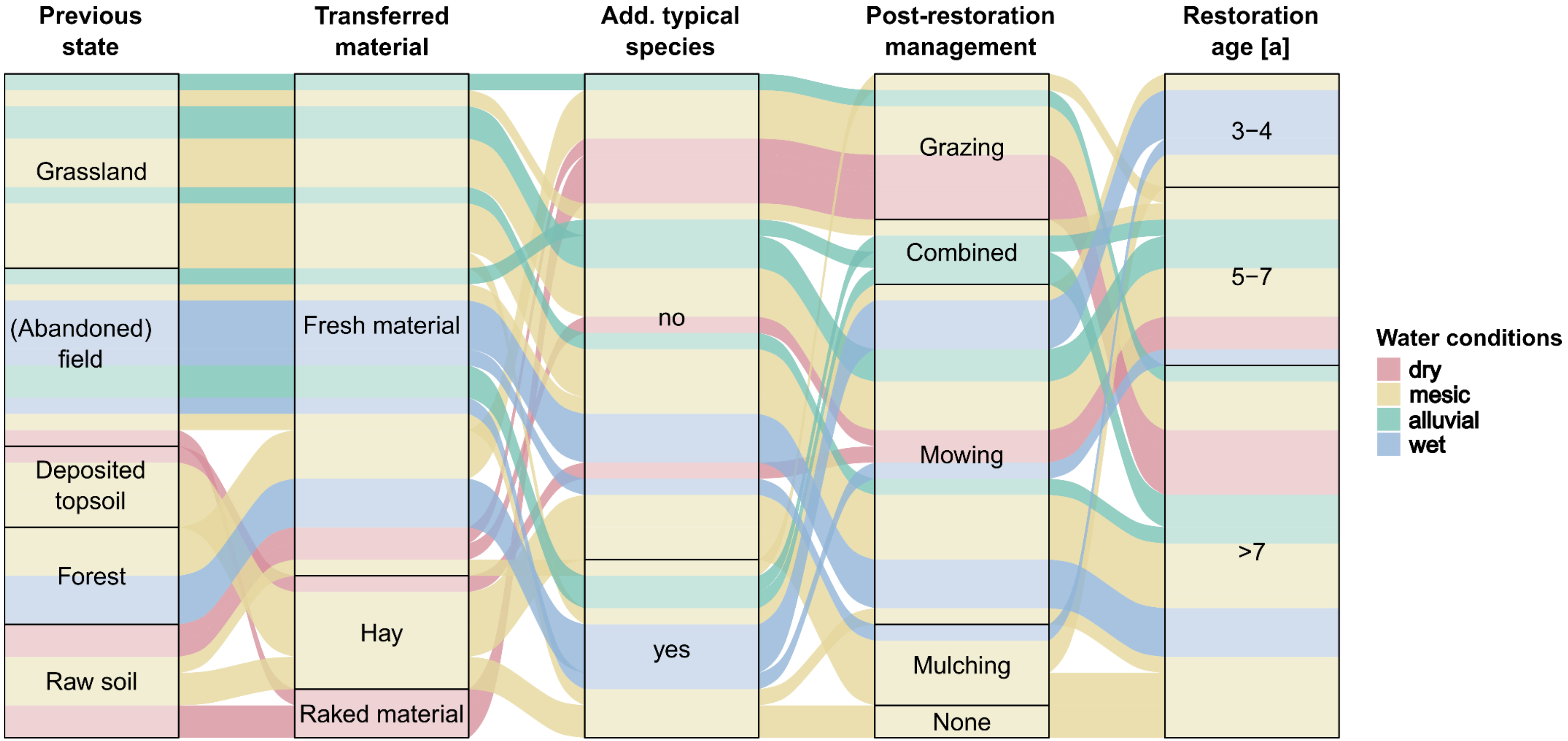

Figure 3.1: Setup of the restoration process for the 41 recipient sites, grouped by the target grassland types as defined by the donor sites (*dry* grasslands, *mesic* grasslands, *alluvial* grasslands with alternating water conditions, *wet* grasslands). The width of each strip represents the proportion 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.

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 ha to 2 ha), or four (> 2 ha) 25 m^2 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 & Wilmanns (1973). Nomenclature followed the German species list (Jansen & Dengler, 2008), version 1.5, and data were organised 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 m^2 squares per plot and merged to 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 $\leq$ 10 days. Deviations from this procedure are listed in Supplement 3.S1. The comparative plot-based vegetation data of corresponding recipient and donor sites are documented in Table 3.S2.

Biomass and soil analyses

After drying at 60 °C for 48 h, 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, USA). 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 $CaCl_2$ 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 analyser (Unicube, Elementar, Germany). The organic C content was calculated as the difference between total C and anorganic 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, 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; twenty 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 m^2,

c) number of typical species per 25 m^2,

d) cover of typical species,

e) number of Red List species per 25 m^2, 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 3.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. 100 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 2-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, species 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 visualised 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 3.1). For analyses on naturalness and hemeroby, see Supplement 3.S2. We chose model types by visually checking the best-fitting response distributions (R package "fitdistrplus", Delignette-Muller et al. 2023). For modelling, 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, Bartoń 2020), we selected explanatory variables for the final models from the following set of variables (see correlations in Figure 3.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 additional introduction of such species was considered. The models with the lowest 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 < 5, indicating no multicollinearity issues. For the generalised 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 mesic grasslands (Figure 3.4B) 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 3.S3, Supplement 3.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 (Figure 3.2A). 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 m^2; Figure 3.2B). Only in wet grasslands were recipient sites markedly more species-rich than donor sites (mean of 40.0 vs. 28.9 per 25 m^2). There was a general trend towards lower numbers and cover of typical and Red List species in the recipient sites compared to the donor sites across grassland types (Figure 3.2C to 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 m^2) 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 m^2, 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 (Figure 3.S2.1 in Supplement 3.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 3.S2.

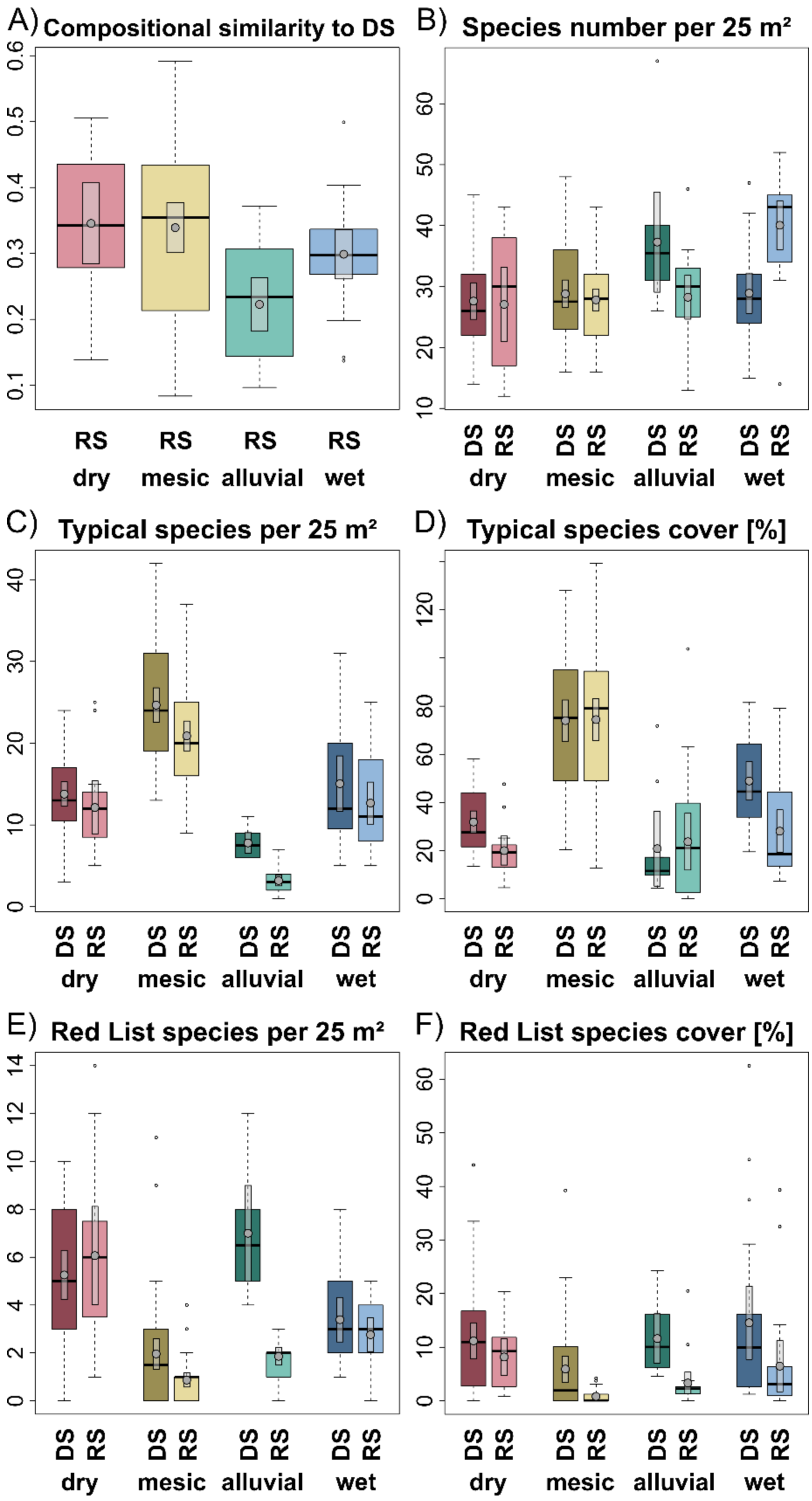

Figure 3.2: Restoration success on the recipient sites (RS) for the different target grassland types – dry, mesic, alluvial, and wet grasslands. In B) to F), data for the donor sites (DS, darker colours) are given in addition to those for the recipient sites (lighter colours). The number of plots (sites) 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 grey points and the corresponding 95 % confidence intervals by the light grey bars.

Abiotic characteristics of donor and recipient sites

Within different grassland types, productivity of donor and recipient sites was similar, with a tendency towards higher productivity of recipient sites of alluvial grasslands (Figure 3.3A). Dry grasslands were less productive than the other grassland types (mean of 109.7 g/m^2 vs. 276.3 g/m^2 dry matter yield). There were trends towards 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 (Figure 3.3B, E, G, H, I). Soil C/N ratios, plant-available K, and soil pH values were similar between donor and recipient sites within grassland types (Figure 3.3C, D, F). The dry grasslands were characterised by more alkaline soils than the other grassland types (mean soil pH of 7.3 vs. 5.3, Figure 3.3F).

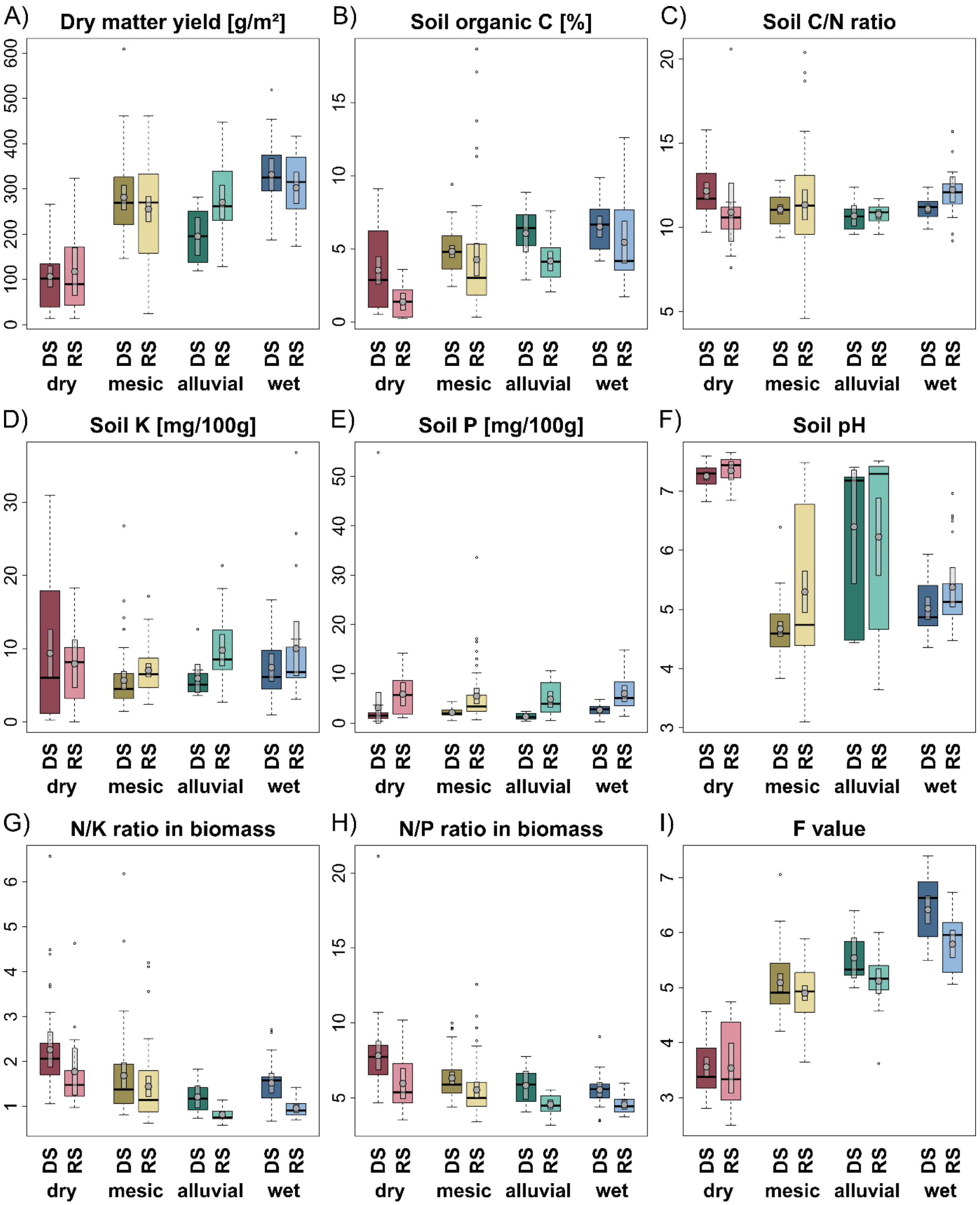

Figure 3.3: Productivity, abiotic conditions, and nutrient stoichiometry of the donor sites (DS, darker colours) of the different grassland types – dry, mesic, alluvial, and wet grasslands – and the corresponding recipient sites (RS, lighter colours). The number of plots (sites) for the eight groups (from left to right) is: 35 (12), 15 (6), 50 (15), 53 (20), 10 (3), 21 (7), 23 (7), 21 (8) (see Supplement 3.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 grey points and the corresponding 95 % confidence intervals by the light grey bars.

Species composition and grassland type-specific success factors

Dry grasslands were separated in two subgroups along the first NMDS axis, which reflected the respective soil conditions (Figure 3.4A). Recipient sites on sandy substrates (nos. 4-6) and their corresponding donor sites had higher Ellenberg L and 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 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 was 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, soil pH) (Figure 3.4B). 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 3.S3, Supplement 3.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 (Figure 3.4C). 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

(Figure 3.4D). 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 3.S1).

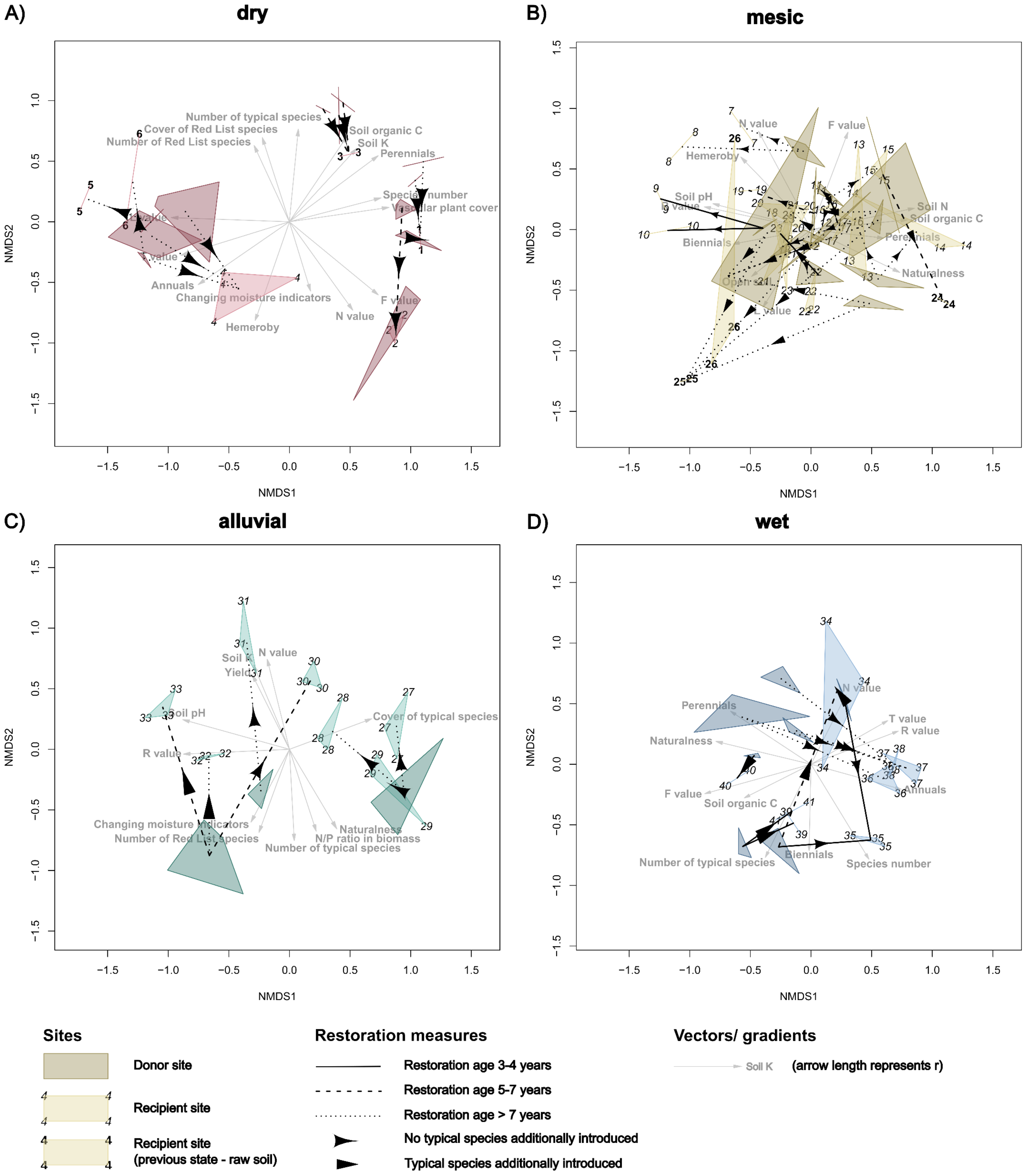

Figure 3.4: Two-dimensional non-metric multidimensional scaling (NMDS) ordinations for the vegetation composition of donor and recipient sites for each target grassland type (A – dry, B – mesic, C – alluvial, D – wet). Sites are symbolised by convex polygons connecting the respective plots, additionally displaying information on the previous state and the numbering (site number at each vertex) of the recipient sites (see legend and Table 3.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 visualisation; see the legend). Grey 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, D) 20.2

Success factors across grassland types

The target grassland types affected restoration success concerning all response variables (Table 3.1). 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 3.S2.1 in Supplement 3.S2).

Table 3.1: 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 modelling 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

	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**
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/100g]		0.362*	0.513***	0.010*	0.041***	0.064**
Soil P [mg/100g]		-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

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 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 favourable, nutrient-poor conditions and low competition for the introduced plant species (Kiehl et al., 2010). Most likely, this was decisive for establishment of many endangered and typical species on the recipient sites (e.g., *Bassia laniflora*, *Globularia bisnagarica*). These findings are in line with literature on restoration of dry grasslands emphasising the reduction of soil fertility to promote target species establishment (Gilhaus et al., 2015; Řehounková 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*, *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 (Biro et al., 2024; Wagner et al., 2021).

In contrast to dry grassland restoration, raw soils did not prove universally favourable 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, Castro Campos, et al., 2023).

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 as 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 $\leq$ 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, Klinger, et al., 2023). As sufficiently low-productive recipient sites are often not available due to nutrient-enrichment in Central European landscapes (Schils et al., 2022; Stevens et al., 2010), 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, Castro Campos, et al., 2023).

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 successful restoration of this grassland type (Breit et al., 2023). Recipient sites 39-41 show that appropriate moisture regimes promote 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 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, Castro Campos, et al., 2023). Our regression models also indicated several other factors 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 establishment of species absent from the donor sites, such as *Betonica officinalis* and *Succisa pratensis* at recipient site 24. In other cases, it appeared to support species with low densities on donor sites, such as *Succisa pratensis* at site 41. This is in line with studies by Baasch et al. (2016) and Hofmann et al. (2020), which demonstrated that additional introduction of target species enables or improves 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, Klinger, et al. 2023). 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 were some dry and very old recipient sites with relatively low species numbers coupled with high proportions of annual species (≥ 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 *Bassia 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 (Sommer, Klinger, et al., 2023; Waldén & Lindborg, 2016).

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, 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 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; Ludewig 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, Klinger, et al., 2023). 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., 2024).

Despite the big advantage of directly investigating practical restoration projects, future research is needed to further support generalisability. 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. Standardised 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.

Author contributions

SH-S, TK, TWD conceived the research idea; LS, SH-S acquired the study sites; LS, NV gathered the data; LS performed data analysis supported by SD, TK, YPK; LS, YPK wrote the first draft of the manuscript; all authors supported LS in editing the manuscript.

Acknowledgements

We thank the German Federal Environmental Foundation for funding the study. We are grateful to G. Gorzejeska and M. Hahn for their help in vegetation recording, and to K. Geißler for acquiring the study sites in one region. We further express our gratitude to B. Biskamp, E. Ollo and L. Pabst for their exertion in soil and biomass sampling and sample processing and to J. Höhl for the lab analyses. Finally, we thank our project partners for supplying suitable study sites and for providing information about the restoration measures taken.

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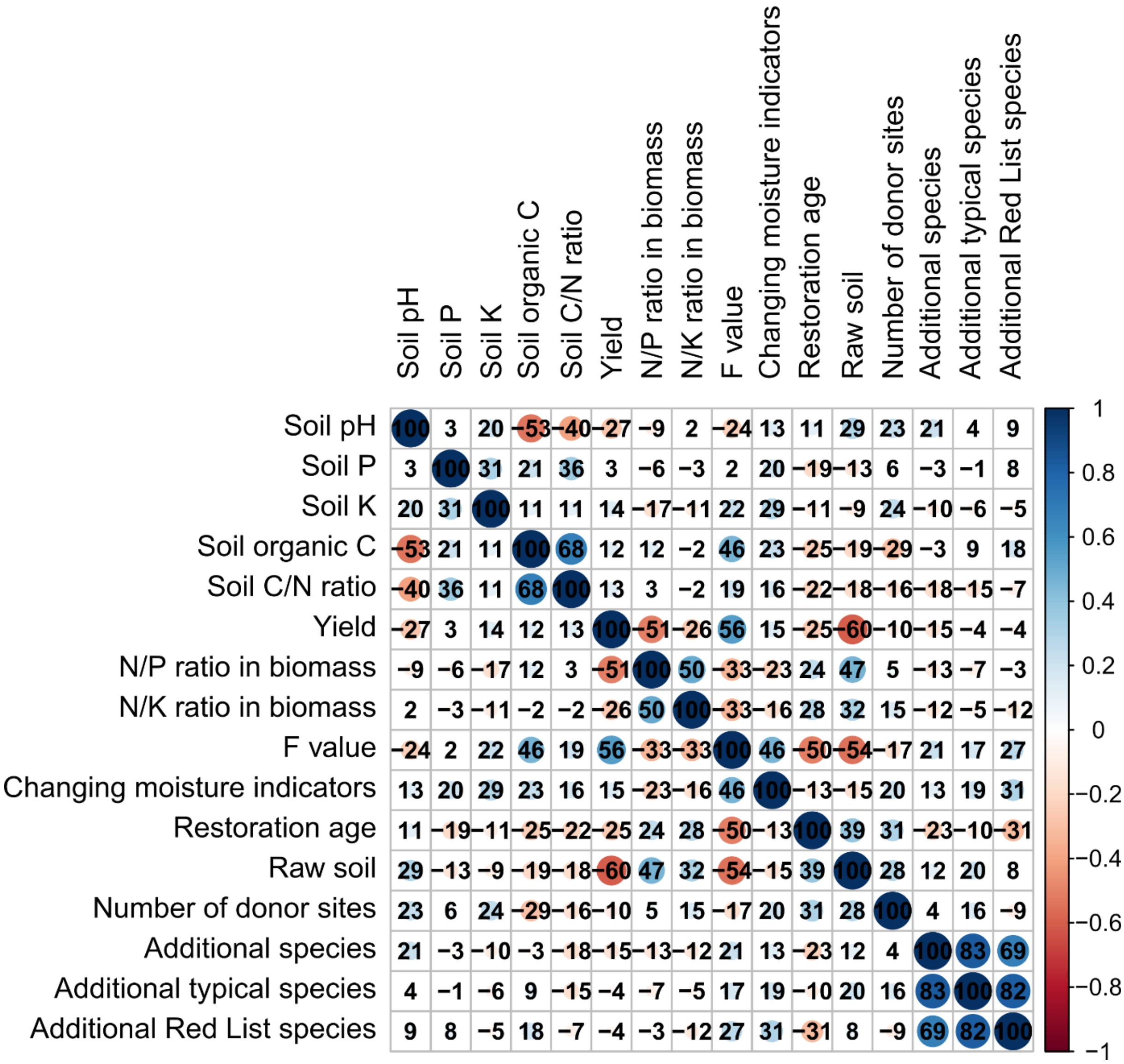
Supplementary materials



	Soil pH	Soil P	Soil K	Soil organic C	Soil C/N ratio	Yield	N/P ratio in biomass	N/K ratio in biomass	F value	Changing moisture indicators	Restoration age	Raw soil	Number of donor sites	Additional species	Additional typical species	Additional Red List species
Soil pH	100	3	20	−53	−40	−27	−9	2	−24	13	11	29	23	21	4	9
Soil P	3	100	31	21	36	3	−6	−3	2	20	−19	−13	6	−3	−1	8
Soil K	20	31	100	11	11	14	−17	−11	22	29	−11	−9	24	−10	−6	−5
Soil organic C	−53	21	11	100	68	12	12	−2	46	23	−25	−19	−29	−3	9	18
Soil C/N ratio	−40	36	11	68	100	13	3	−2	19	16	−22	−18	−16	−18	−15	−7
Yield	−27	3	14	12	13	100	−51	−26	56	15	−25	−60	−10	−15	−4	−4
N/P ratio in biomass	−9	−6	−17	12	3	−51	100	50	−33	−23	24	47	5	−13	−7	−3
N/K ratio in biomass	2	−3	−11	−2	−2	−26	50	100	−33	−16	28	32	15	−12	−5	−12
F value	−24	2	22	46	19	56	−33	−33	100	46	−50	−54	−17	21	17	27
Changing moisture indicators	13	20	29	23	16	15	−23	−16	46	100	−13	−15	20	13	19	31
Restoration age	11	−19	−11	−25	−22	−25	24	28	−50	−13	100	39	31	−23	−10	−31
Raw soil	29	−13	−9	−19	−18	−60	47	32	−54	−15	39	100	28	12	20	8
Number of donor sites	23	6	24	−29	−16	−10	5	15	−17	20	31	28	100	4	16	−9
Additional species	21	−3	−10	−3	−18	−15	−13	−12	21	13	−23	12	4	100	83	69
Additional typical species	4	−1	−6	9	−15	−4	−7	−5	17	19	−10	20	16	83	100	82
Additional Red List species	9	8	−5	18	−7	−4	−3	−12	27	31	−31	8	−9	69	82	100

Figure 3.S1: Correlation coefficients of the explanatory variables tested in the model selection process for cross-grassland success factors of restoration. For better readability, correlation coefficients in the matrix are given as percentages. In accordance with the linear (mixed) models, raw soil, additional species, additional typical species, and additional Red List species were turned into Boolean variables. For the “yes” state, their values were set to 1, and for the “no” state, their values were set to 0, respectively.

Supplement 3.S1: Deviations from default course of action and missing values.

One donor site and three corresponding restoration sites were investigated already between 17 May and 4 June 2021, all before the first cut or grazing. The maximum timespan between the sampling dates of these sites thus amounted to 18 days. The sampling scheme of the four sites followed our default, with the exception that only three 25 m^2 plots per site were investigated although three sites were larger than 2 ha. As we did not expect strong impacts on the quality of our analyses, we included the obtained data as they were.

For six plots sampled in 2022, biomass samples were lost at different process stages, resulting in missing data for yield and/ or nutrient contents.

For one plot, no average height of the upper herb layer was measured, resulting in a missing value.

One donor site had already been mown at the time of the planned sampling so that biomass samples were taken from the windrowed cuttings close to the plots, and no yield was calculated. The species composition of this site was recorded from the re-grown vegetation on the 12 August 2022, which presumably led to an underrepresentation of grass species. However, as we did not expect major impacts on our analyses, we included these vegetation data. Structural parameters (cover of different layers, growth height) for this site were excluded from the analyses.

On one restoration site, low-intensive cattle grazing had already started about one month before our sampling. As the aboveground biomass appeared not to have been strongly reduced yet, sampling was carried out following the default procedure, and all data were included in the analyses.

Supplement 3.S2: Methods and results of the analyses on naturalness and hemeroby.

As this supplement has its own literature list, find it in the “Supporting Information”, there named as Supplement S2, of the original research article:

Sommer, L., Donath, T. W., Harvolk-Schöning, S., Kleinebecker, T., Schneider, S., Voß, N., & Klinger, Y. P. (2025). Grassland restoration practice in Central Europe: Drivers of success across a broad moisture gradient. *Restoration Ecology*, 33(7), e70106. https://doi.org/10.1111/rec.70106

Table 3.S1: Investigated recipient sites with information on the locations, donor sites, restoration measures, site conditions, and restoration success.

Due to the large format of this table, find it in the “Supporting Information”, there named as Table S1, of the original research article:

Sommer, L., Donath, T. W., Harvolk-Schöning, S., Kleinebecker, T., Schneider, S., Voß, N., & Klinger, Y. P. (2025). Grassland restoration practice in Central Europe: Drivers of success across a broad moisture gradient. *Restoration Ecology*, *33*(7), e70106. https://doi.org/10.1111/rec.70106

Table 3.S2: Vegetation data of the 41 recipient sites in comparison to their corresponding donor sites.

Due to the large format of this table, find it in the “Supporting Information”, there named as Table S2, of the original research article:

Sommer, L., Donath, T. W., Harvolk-Schöning, S., Kleinebecker, T., Schneider, S., Voß, N., & Klinger, Y. P. (2025). Grassland restoration practice in Central Europe: Drivers of success across a broad moisture gradient. *Restoration Ecology*, *33*(7), e70106. https://doi.org/10.1111/rec.70106

Table 3.S3: Overview of the (generalized) linear models selected for the variables of restoration success in mesic grasslands. In the first two rows, the assumed response distribution and the R package used for modelling 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 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 number of observations and the R^2 of the models are given.

	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	-0.846*	28.750***	24.145***	1.290***	2.426**	-4.691***
Intercept (ZI model)						-0.197
Soil C/N ratio					-0.216**	
Soil organic C [%]					0.185**	
Soil K [mg/100g]						0.077*
Soil P [mg/100g]						
Soil pH	-0.172**		-1.491*	-0.139***		0.226*
Dry matter yield [g/m^2]	0.002**		0.017	0.001***	-0.004*	
N/K ratio in biomass	0.296***					
N/P ratio in biomass						
Multiple donor sites (y/n)					-1.049	
Raw soil (y/n)	-1.080***	-5.464*	-5.875			2.309***
Add. species (y/n)	0.446*		n.c.	n.c.	n.c.	n.c.
Add. typical species (y/n)	n.c.	n.c.	5.474*		n.c.	n.c.
Add. Red List species (y/n)	n.c.	n.c.	n.c.	n.c.		-1.434***
Restoration age [a]				-0.011		-0.172***
Number of observations	51	51	51	51	51	51
R^2	0.530	0.083	0.289	0.572	0.319	0.031

Chapter 4: Grassland restoration with plant material transfer – bridging the knowledge gap between science and practice

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2023, *Global Ecology and Conservation*, *47*, e02638. doi: 10.1016/j.gecco.2023.e02638

Abstract

In Central Europe, species-rich grasslands have strongly diminished over the last century. The transfer of seed-containing plant material from donor sites with a desired species composition to restoration sites is a well-established method to restore species-rich grasslands. Despite a plethora of available literature, restoration projects with plant material transfer often fail or do not reach the planned goals. Practitioners' knowledge is a highly important but underexplored source of information on factors deciding about success of restoration projects. At the same time, it is unclear to which degree scientific findings on success factors are known and considered by practitioners, and if science actually investigates the most relevant aspects for practice. To bridge the gap between practitioners' knowledge and restoration science, we conducted semi-structured interviews with 33 practitioners involved in plant material transfer projects. Using qualitative content analysis, we analysed the interviews for success factors, and compared them to success factors of plant material transfer as investigated in peer-reviewed European studies on the method. We found that science investigated a broad range of practical, technical, and ecological success factors, and that practitioners were generally well aware of this evidence, trying to make use of the knowledge. Failure of practitioners' projects often resulted from organizational obstacles, which were founded in lacking trust and low experience levels among the involved people. We advise unexperienced practitioners to involve more experienced practitioners in their projects if possible. Furthermore, we emphasize the importance of identifying relevant local stakeholders and building trustful regional networks. Interdisciplinary scientific studies considering success factors beyond practical and ecological aspects are required to support widespread effective grassland restoration with plant material transfer.

Keywords

plant material transfer, hay transfer, success factors, semi-structured interviews, communication, experience

Introduction

Semi-natural grasslands of the temperate zones are among the world's most diverse ecosystems (Wilson et al., 2012), providing multiple ecosystem services (Bengtsson et al., 2019; Chapin et al., 2000) and high aesthetic value (Lindemann-Matthies et al., 2010). Abandonment of agricultural use, conversion to arable fields, and intensification have strongly decreased the quantity and quality of these habitats in Europe over the last century (Habel et al., 2013; Schils et al., 2022). With the ecological state still deteriorating (*EU COMMISSION*, 2020), ecological restoration of semi-natural grasslands in Europe is urgent (Török et al., 2011; Waldén & Lindborg, 2018).

Plant material transfer, i.e., the transfer of freshly cut or dried seed-containing hay is a widely used method to restore species-rich grasslands (Kiehl et al., 2010). During seed maturity of target species, the plant material is collected from a species-rich donor grassland and transferred to the restoration site. In the best case, the transferred diaspores provide the basis for a species-rich grassland community similar to the donor community. A major advantage of plant material transfer is its independence from the availability of site-specific regional seed mixtures, whose low availability is still a major constraint in grassland restoration (Dolnik et al., 2022). If freshly cut plant material is transferred, cryptogams and invertebrates may be transferred in addition to vascular plant species, which is considered advantageous compared to other methods, such as sowing of seed mixtures, brushed or threshed seed material (Kiehl et al., 2010; Michalska-Hejduk et al., 2017; Stöckli et al., 2021). The application of plant material transfer is therefore desirable from an ecological perspective.

Spreading knowledge about the advantages of plant material transfer to the public, e.g., via compendiums (Harnisch et al., 2014; Hölzel, 2007) or workshops, has contributed to its relevance in practical grassland restoration today. At a conservation workshop in Germany in late 2020 and in a follow-up interview, two of the authors talked to an employee of a nature conservation authority, to whom we refer as Paul. He had recently been tasked with restoring a species-rich floodplain meadow on a former arable field, and wanted to use plant material transfer. Having little experience, Paul read relevant literature (e.g., Hölzel, 2007) and looked for information in the internet. This way, he learned about success factors, i.e., aspects that, if addressed, can improve the outcomes of plant material transfer projects. Accordingly, as an important condition (Török et al., 2011), he identified a nearby species-rich floodplain meadow as a suitable donor site, and agreed with the farmer to use material from this site for restoration. However, several unexpected difficulties emerged in the course of the project. First, project planning only started in spring, so that the site had already been cut, and Paul decided to use material from the second cut in autumn instead. However, a severe summer drought occurred that year, and there was far too little plant material available to cover the whole restoration site. Thus, Paul, who felt urged to carry out the measure in that year, decided to additionally spread chopped hay on the restoration site, relying on the cooperating farmer's statement that the hay originated from "low-intensively managed" grassland sites. Paul admitted that with this unknown seed source, it is likely that the restoration measure has led to a suboptimal outcome, although no monitoring results were available at the time of our interview.

Given the alarming ecological state of semi-natural grasslands in the European landscape, successful restoration of species-rich grasslands is essential. Despite increasing awareness for the topic as well as growing scientific knowledge on relevant success factors (e.g., Slodowicz et al., 2023; Sommer et al., 2023), practical grassland restoration projects with plant material transfer often deviate from the desired courses of action, as Paul's example demonstrates. At the same time, it is unclear to which degree practitioners base their actions on the existing scientific evidence on relevant success factors, and if science considers the questions relevant to practitioners. We interviewed practitioners who performed restoration projects using plant material transfer and analysed their responses, aiming at answering the following questions with respect to relevant scientific literature:

1) To which degree have the success factors of plant material transfer relevant for practitioners been investigated and confirmed by science?
2) Which success factors mentioned by the practitioners are beyond the previous scope of science?
3) What strategies can practitioners employ to improve future outcomes of grassland restoration projects with plant material transfer?
4) How can science contribute to this?

Methodology

To better understand the process of plant material transfer and relevant success factors from the practitioners' perspective, we conducted semi-structured interviews with 33 practitioners between November 2020 and September 2022. Qualitative content analysis (Kuckartz, 2018) was used to systematically analyse and code the data from the interviews.

Selection of interview partners

Initially, we contacted and interviewed 18 practitioners involved in plant material transfer projects. At the end of each interview, all initial partners were asked to name further practitioners using plant material transfer. From these, 15 could be engaged for an interview. Two of the 31 interviews were performed with two practitioners, 29 with one practitioner.

The final panel comprised practitioners from nature conservation and road construction authorities (9), landscape planning offices (7), publicly funded project offices (7), farms (5), landscaping agencies (3), and compensation agencies (2) (Table 4.S1). They were involved at different stages of the projects, i.e., in planning or organization (28 practitioners), realization (9), monitoring (13), or post-restoration management (5). The practitioners had different experience levels and were involved in the restoration of a range of grassland types (Table 4.S1). The restoration projects were located in Germany, Switzerland, and Luxembourg.

Conduction and content of interviews

The semi-structured interviews were conducted via video call (25 partners) or in person (8 partners). Interview length ranged between 43 and 127 minutes per partner, and the interviews were recorded. This resulted in 44 hours of audio material. We started each interview by asking for the practitioners' understanding of the term "plant material transfer" (German "Mahdgutübertragung") and their experiences with the method. As there were different attitudes if the term "Mahdgutübertragung" refers only to the transfer of fresh or also of dried mown plant material, we asked the interview partners to talk about both approaches. If applicable, we also asked to talk about the transfer of raked plant material (German "Rechgutübertragung"), which was done in the restoration of calcareous sandy grasslands. If the practitioners did not cover the following topics comprehensively by themselves, we asked about them directly:

- reasons for choosing the method of plant material transfer
- aims of the project(s), financing, organization, setup of the project(s)
- practical implementation of plant material transfer (when and how), complementary restoration measures

- post-restoration management
- evaluation of success, decisive factors for success, options for improvements of success
- used sources of information on plant material transfer, sharing of know-how and experiences
- further need for research

By covering these different aspects, we made sure to get a detailed understanding of how the practitioners' projects were set up on the practical and organizational level, and we got a sense of the involved people's attitudes towards their projects.

Analysis of the interviews

We transcribed the interviews in the form of detailed notes, i.e., not word for word, but we noted down the gist of every of the practitioners' statements. Memorable or emotional phrases were transcribed word for word. Following the guide of Kuckartz (2018), we then conducted a qualitative content analysis that reflected the aims of our research.

In a first step, we went through the transcripts and coded success-related text segments, i.e., statements on project goals and on factors that seemed decisive for success in the practitioners' minds. We derived a preliminary set of 56 different success factors and attached them to the coded text segments, using the software QDA Miner Lite (Provalis Research, 2018). In this way, we gained a first overview of the aspects the practitioners considered important, and of typical wordings or phrases they used to describe success factors for plant material transfer. Examples for such wordings are:

- "[...] is/ was important/ decisive"
- "one has to pay attention to [...]"
- "it has to be done like [...]"
- "[...] is/ was a sticking point"
- "I would change [...] next time"
- descriptions of causes and effects with respect to project success

In a second step, we re-read the transcripts, and re-coded them for success factors, which was facilitated by the impressions we had gained from the first round. We coded additional text segments as success factors, removed codes where it became evident that a clear success relatedness was missing, and split success factors into more specific "sub-factors" to facilitate content analysis. In this way, we identified 173 success factors. These were then grouped into 17 categories. While some of the categories represent the different stages of the rather fixed and sequential process of plant material transfer, other categories include success factors that affect the process as a whole (see “Results” section, the complete coding is given in Table 4.S2 in the Supplementary material).

Results

Project goals and success factors addressed by the practitioners

While the practitioners had strong overlaps in their project goals and consistently mentioned a range of relevant success factors, we also found a broad variety of aspects to consider. The establishment of rare or regionally typical target plant species and plant communities was the main goal of the practitioners' projects. However, faunistic conservation goals, such as protection of ground-nesting birds or support of invertebrates, also played a role. Depending on the restoration context, ensuring usability as fodder was important, or, in case of dykes and road embankments, erosion control.

Out of the 17 success factor categories, harvest and transfer of plant material, environmental impacts, and project organization were the most frequently addressed ones (by 26, 25 and 24 of the 33 practitioners, respectively; Figure 4.1A). Among the full list of 173 success factors, low nutrient supply on the restoration sites, weather conditions after restoration, and building on own experiences over time were most frequently mentioned (by 19, 15 and 13 practitioners, respectively; Figure 4.1B). The original quotes in German language, the full coding and coding frequencies are given in Table 4.S2.

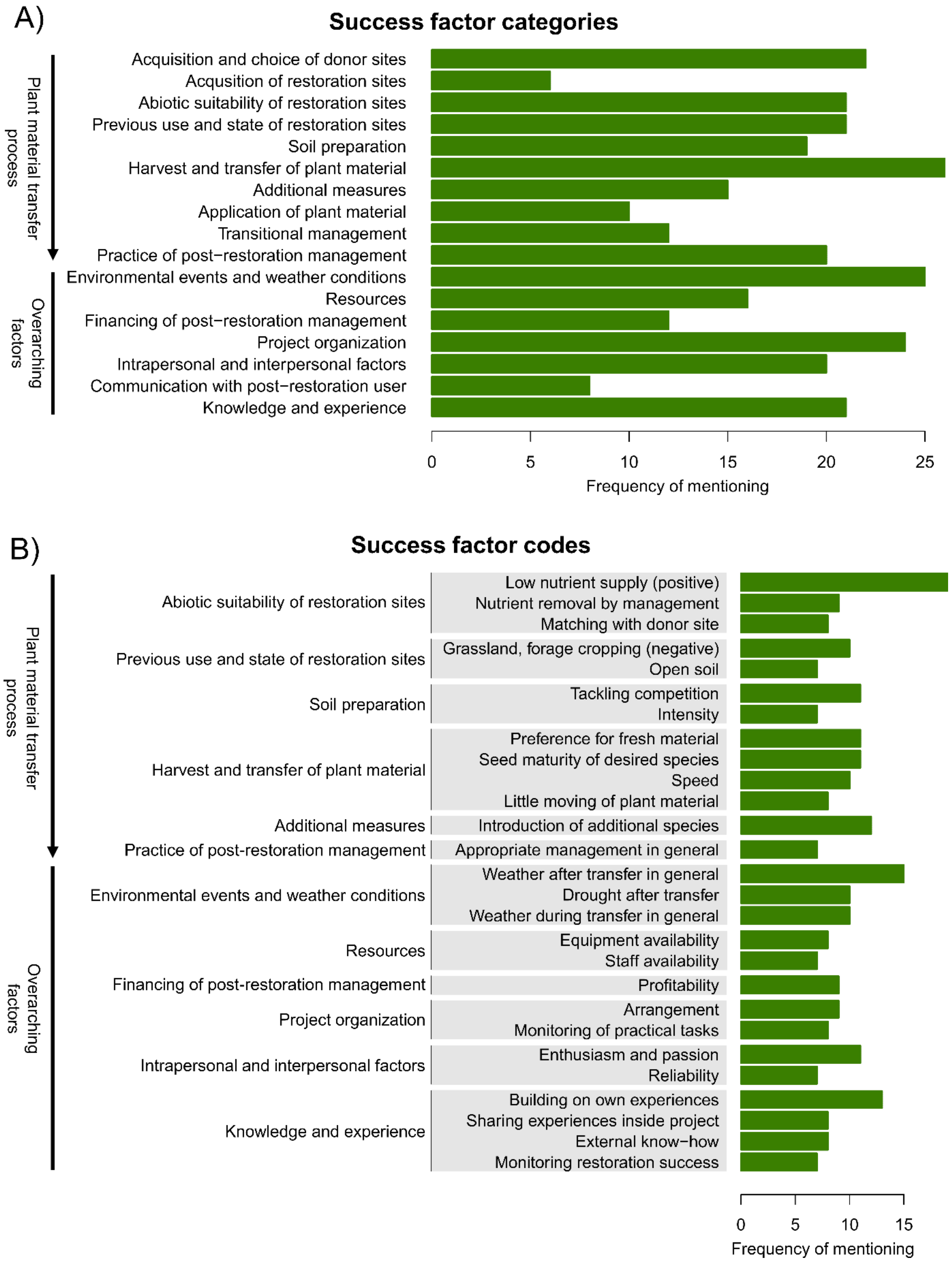

Figure 4.1: Frequencies of success factors as mentioned in the interviews with the 33 practitioners. Number of practitioners who addressed each of the 17 success factor categories (A) and each of the 27 most frequent success factor codes (B, category names to the left of the grey-shaded codes). The process-related factors/ categories are ordered accordingly in (A) and (B), the plant material transfer process is indicated by the black arrow on the left, respectively. Below, the frequencies of the overarching success factors/ categories, i.e., those affecting the restoration process as a whole, are given. Frequencies of all success factors are given in Table 4.S2.

Process-oriented view on the success factors

We developed a framework in which the various success factors and their complex relationships are ordered according to the process plant material transfer (Figure 4.2). In the following, we explain the different stages and aspects of our framework, going into detail about most success factors, supporting our explanations with translated quotes. The success factors linked to each of our statements and of the example quotes are indicated by their abbreviations in brackets, and can be seen in detail in Table 4.S2. Additionally, the practitioners cited are given in italics after the quotes. Success factors that were addressed by only a few partners and appear to be less relevant are not included in the text (but in Table 4.S2).

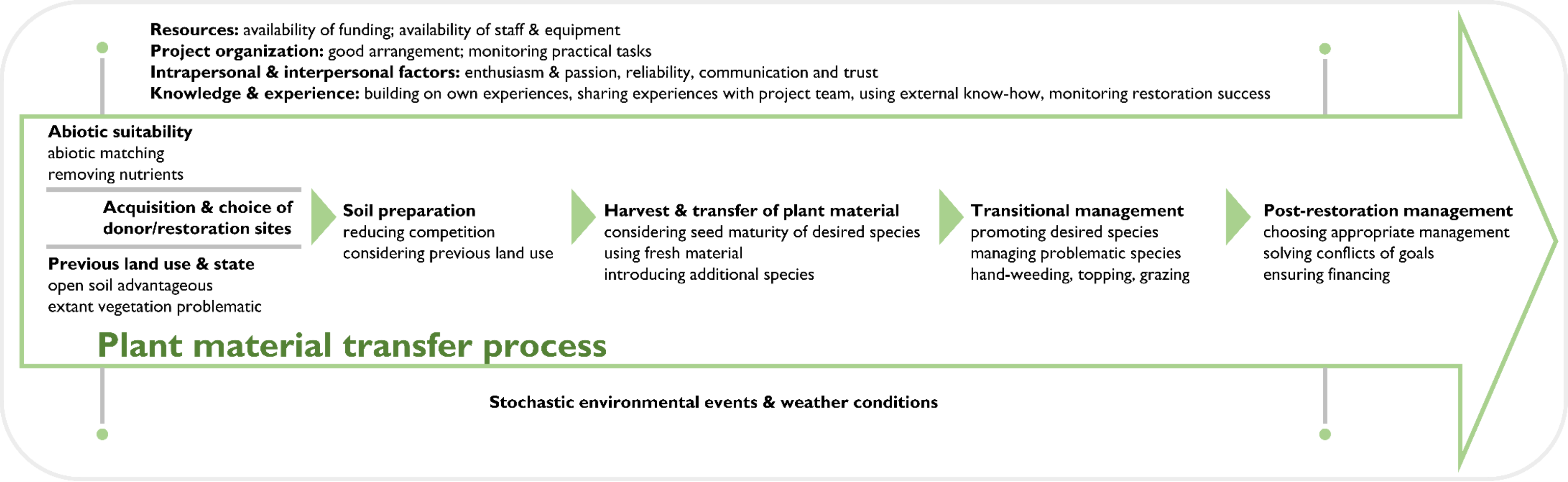

Figure 4.2: Factors affecting the success of plant material transfer according to the 33 interviewed practitioners. Factors related to a certain step of the process of plant material transfer are placed inside the arrow, their chronological order is from the left to the right. Overarching factors, i.e., factors affecting the plant material transfer process as a whole, are placed outside the arrow.

Acquisition and choice of donor sites

As a main motivation for restoration, practitioners mentioned the drastic losses and, thus, scarcity of species-rich grassland sites in their regions. Accordingly, knowledge and availability of suitable donor sites as plant material sources were often considered a bottleneck, which was met in different ways.

Prominently, donor site quality was considered crucial: *"First, you need enough donor sites. These shouldn't be just species-rich, but also should not contain problematic species. [...] In [our federal state], we hardly have species-rich grasslands in [...] agricultural use any more"* (quote from practitioner *PFPO6*; success factor DS04; see Table 4.S2). To facilitate material transport, proximity to the restoration sites was considered important (DS01). Furthermore, the practitioners emphasized that donor sites should be sufficiently large to provide enough plant material (DS09). Several times, it was mentioned that great attention should be paid to suitable management of potential donor sites in a region to keep their diversity (DS07). Monitoring donor sites concerning the presence and abundance of desired and undesired species was considered relevant, too (DS06). To this end, sites with poisonous species or weeds should be excluded from harvest, or the plants should be removed: *"You have to take care not to transfer [Jacobaea vulgaris] or [Rumex obtusifolius]; we weed them before harvest"* (*PFPO3*; DS05).

To get access to suitable donor sites, many practitioners relied on their local knowledge of sites and positive relationships with the managing farmers (DS02; DS08). While donor site databases could facilitate acquisition (DS03), practitioners were also worried about competition: *"The question [is] if we should have a donor site database or not. You get a competitive situation. We already notice that [another practitioner] snaps up the donor sites that we've been using for years"* (*LSPO7;* DS13). There was agreement that when grasslands managed by farmers are used as donor sites, adequate compensation for the biomass is important: "*We compensate the farmer, that's important for acceptance. [Our payment] is not staggering, but it's a good, fair price*" (*PFPO2*; DS11).

Acquisition of restoration sites

When acquiring restoration sites, practitioners were often confronted with land use pressure and competition with farmers' interests. If purchase of sites for restoration was not possible, practitioners relied on respectful talks with the managing farmers.

Many practitioners who tried to purchase sites for restoration considered limited availability a big challenge: *"Access to sites would be desirable [...]. There are enough arable fields in the floodplain, but acquiring sites is extremely difficult. The [federal state] government could, for example, buy sites [...] and make them available for restoration"* (*FARM3*; AR02). If restoration of grasslands managed by farmers were planned, practitioners emphasised the importance of respectful talks: *"[One should] communicate with the farmers early, before displeasure grows and becomes unstoppable. […] Presenting [restoration] as an offer is very important, that you don't impose anything [and show] appreciation for the farmers' work"* (*PFPO4*; AR04). Price gradations for restoration sites were mentioned depending on agricultural usability. If grasslands with site conditions unfavourable for intensive agricultural use, e.g., wet meadows, were to be restored, prices of restoration sites were often lower compared to more favourable sites (AR03).

Abiotic suitability of restoration sites

As practitioners pointed out, suitability of a restoration site to support a target plant community crucially depends on abiotic conditions, which have to be carefully considered in project planning.

Aspects mentioned as decisive for success were suitable nutrient levels (SR04-SR06), soil pH (SR08), hydrological conditions (SR10, SR11), exposure, and slope (SR12). Several practitioners based their assessments on abiotic similarity to the donor sites (SR02), partly underlining the importance of soil analyses (SR03). For example, one practitioner reported problems with restoring grasslands on dykes because of unknown site conditions: *"Ideally, the topsoil is stored separately for different sides of the dyke and re-used accordingly. But sometimes a [highly fertile] sugar beet soil is deposited, then you have a lot of [Mercurialis annua]. And sometimes, the soils are humus-free and do hardly become green"* (*LSCG2*; SR17). Generally, low nutrient levels were seen as beneficial to restoration success: *"[The restoration sites] have become very rich in flowers, with many forbs and very low vegetation cover. But this was due to the poor [nutrient level]"* (*PFPO7*; SR04). To reduce nutrient levels, practitioners mentioned topsoil removal as an effective and quick tool (SR18), while management (SR07) was often seen as a time-consuming and less effective instrument:

> *"We wanted to remove the topsoil from the field. […] We've calculated that [otherwise], with 10 mg phosphorus per 100 g of soil, from which we wanted to get down to 5 mg/ 100 g, at least ten years of intensive use with high N fertilization would be required to get somewhat in that direction. So saying that you do one year of intensive arable use […] and do plant material transfer in the following year, that's eyewash, a myth"* (*LSPO7*; SR07).

In some cases, successful outcomes were observed on initially nutrient-rich sites, possibly because of N-limitation due to nitrogen leaching (SR06). However, nutrient-poor site conditions are not always desirable, as low productivity may negatively affect post-restoration use and development of target grassland communities. One practitioner warned: *"There is that idea […]*

that the site should be as nutrient-poor as possible, and then plant material transfer projects are planned on pure gravel sites. As if any low-productive meadow would grow on washed gravel" (*LSCG1*; SR05).

Previous use and state of restoration sites

Previous use of a restoration site determines the level of competition that transferred species are confronted with, and is therefore another decisive success factor.

Closed swards of grasslands or multiannual fodder crops were considered particularly challenging (PR06), and restoration without topsoil removal even seemed pointless to some practitioners: "*I've said goodbye to the idea of introducing species into existing grassland. If so, you need [...] a successional restart. If I was dealing with floodplain meadows, I would do it like [another practitioner who applied topsoil removal]*" (*AUTH9*; PR14). Due to lacking competition, raw soils, e.g., in mining areas were generally seen as advantageous (PR15). In restoration of calcareous sandy grasslands, substrate application was considered very effective to create raw soils, with the additional opportunity to regulate abiotic conditions: "We *only take sand from a depth of more than 2 meters, because above that, it can contain root pieces [of undesired species], and can be decalcified. We had bad deliveries [...], which contained e.g., root pieces of [Ailanthus altissima], which grows very quickly then*" (*FARM5*; SR15, PR18). Sometimes the expression "raw soil" (German "Rohboden") was used colloquially, actually referring to humus-containing open soil, e.g., on arable fields (PR01, PR02) rather than to minimally developed soils. These also offer conditions with low competition by existing vegetation: "*Over the last years, we've almost exclusively [restored] cleared arable fields, so that [we've hardly needed] any site preparation.*" (*AUTH3*).

Soil preparation

Many practitioners advocated soil preparation prior to plant material application, but some concerns and questions regarding necessity and negative side effects were also raised.

While creating a good seedbed for germination was an important goal of soil preparation (SP02), tackling competition by the existing vegetation was very prominent: "We've *made the experience that the more intensely you disturb the soil and destroy the competing vegetation, the more successful your measure gets*" (*LSPO6*; SP03, SP11). However, for some subsequent users of restored meadows, uneven soil surfaces from ploughing were an obstacle: "*Some sites had been ploughed. I had suggested to [the planner] to level them… but no, the seeds wouldn't sprout so well then. That's like a mogul field, you ram against those bumps with your mower afterwards*" (*FARM2*; SP01). Two practitioners reported diminishing effects of soil preparation on species establishment in the long-term (SP15). Furthermore, negative side effects of soil preparation on insects or target plant species already present on existing grassland were mentioned (SP13).

Harvest and transfer of plant material

Practitioners were concerned with transferring as many seeds of desired species as possible when harvesting, storing, and transporting plant material, while affecting germination as little as possible.

Many practitioners aimed at optimizing the harvest date: "*If I harvest [...] in June, I only have grasses. The donor site vegetation must be recorded, you need the right timing. I have to look which species have shed their seeds, which ones are ripe, which ones are flowering*" (*PFPO7*; HT02, HT07). Having access to different donor sites allows for flexibility: "*The donor site had been mown before [our planned] harvest, as the farmer had forgotten about it. Then you have to react quickly to find an alternative*" (*PFPO3*; DS10, HT09, HT10). Some practitioners harvested at several dates to transfer more species (HT05), whereas many preferred additional sowing or planting of target species to make organization less complicated (AM01). In hay transfer on dykes or road embankments, nurse crops such as cereals or *Bromus secalinus* were added to achieve fast sward closure and erosion control (AM04).

There was broad agreement that transferring freshly cut material is, in principal, preferential to transferring dried material, even among practitioners who often applied the latter method: "*Surely, fresh material is better by factor three. Due to withering, windrow and so on you have considerable losses [of seeds] in hay bales. Interestingly, many of the early and late flowering species get established, but surely less than with fresh material*" (*LSCG2*; HT13). One reason to use hay bales was that seeding on large restoration sites is easier to organize, as material from different donor sites can be combined (HT14). Another practitioner appreciated that hay bales enable hydro-seeding on steep road embankments, as they can be shredded and mixed with moisture holders for adherence, and sprayed on the embankments (AP02).

Mowing during wet conditions, e.g., in the early morning, was recommended several times to increase seed capture (HT12). Many practitioners emphasised that the plant material should be moved as little as possible prior to collection (HT16) and considered rapid transfer of fresh material crucial to minimize seed losses: "*Optimally, we mow and load the plant material onto the silage wagon without any delay*" (*PFPO4*; HT17). There was uncertainty on the effects of hay storage on seed quality: "*I store [the bales] for two years at maximum, I've no idea about the germination ability. The danger of losses is high. The bales are under fleece, but are exposed to weather conditions*" (*LSCG2*; HT18).

Transitional management

In the first years after restoration, many practitioners were confronted with the emergence of undesired species, which were not part of the target plant communities. To direct plant communities towards the target states, specific transitional management was often considered crucial.

As outlined before, poisonous species or weeds occur on freshly restored sites depending on abiotic conditions, previous state, site preparation, and plant material composition. Eliminating unwanted species is so important that sometimes hand-weeding was performed (TM01). A central transitional management practice was topping (German "schröpfen"), i.e., cutting to weaken fast-growing weeds and prevent them from developing ripe seeds: *"[The initial management in the first years] must not be based on the later regular management. In front of students, I have also advocated not to follow any faunistic arguments or conservation dogmas with late cutting […]. Mowing, mowing, mowing leads to success"* (*LSPO7*; TM03). In the eyes of some practitioners, increased nutrient richness and productivity required more frequent topping and biomass removal over longer time periods (TM05, TM06). Intensive grazing was mentioned as another option to suppress undesired species such as *Cirsium arvense* (TM02). Several practitioners recommended monitoring during the first years: *"Finding the optimal management is definitely a permanent issue and very challenging. You have to observe all the time how the vegetation reacts, and then adjust the management, ideally jointly with the farmers"* (*LSPO3*; TM08).

Post-restoration management

To maintain a stable plant community after transitional management, adapted post-restoration management was an important success factor for many practitioners. However, management often had to make compromises due to limited funding and different, sometimes conflicting conservation goals.

Some practitioners stressed the relevance of management in general, as opposed to leaving restored sites unmanaged (PM01). Others specified the need of low-intensive management, as opposed to intensive agricultural exploitation (PM02). Management that can be refinanced by biomass use, e.g., as livestock fodder, was often seen as the best option to secure the conservational value of restoration sites. However, this was hard to reconcile with low-intensive management: *"If the barn for 200 cows is financed and then you […] tell [the farmer], 'Just try low-intensive management', that's a complete changeover for the farm. […] Contractual nature conservation is not sufficient there; the cows have to be fed."* (*PFPO4*; FM01, FM02). In some cases, practitioners reported severe failures in post-restoration management. For example, to improve fodder values of restored sites, some farmers tilled and re-sowed restored grasslands with commercial seed mixtures (PM12, PM13).

Given that low-intensive management could be implemented, the decision for mowing or grazing management was a big topic. Mowing was often advocated with regard to certain target plant communities: *"My impression is that [in our federal country] too little attention is paid to [management]. For reasons of cost [reduction], people try to maintain systems by grazing that have actually evolved from mowing"* (*LSPO6*; PM03, PM09). If mowing was chosen, adaptation of the cutting regime to the needs of certain target species or species groups was important (PM06). This often resulted in conflicts between different restoration goals: *"The cutting date […] was postponed […] to protect ground-nesting birds. That's not favourable with regard to [the invasive plant species Solidago canadensis]."* (*LSPO2;* PM07). Grazing was advocated for different reasons, e.g., for its potential to suppress undesired species, to achieve higher structural diversity, and to create germination gaps for target plant species:

> *"The thistles have almost disappeared because of the sheep [grazing]. […] We observe decline of [Peucedanum offcinale] after plant material transfer [if there is only mowing]. [This target species] certainly needs regular soil disturbance. […] Perhaps, one would have to go in there with larger grazers. […] Certainly, a richer mosaic would be good in the sites"* (*FARM5*; PM04, PM08, PM10).

Stochastic environmental events and weather conditions

Environmental conditions before, during and after restoration affected the outcomes of many projects, with major impacts by stochastic events. The practitioners' main strategy of dealing with this problem was repetition of plant material transfer.

Several practitioners mentioned negative consequences from flooding for plant material transfer in floodplain meadow restoration: *"If you have a donor site in the active floodplain which is flooded over the summer, your measure is already dead for that year"* (*AUTH7*; EN02, EN04). The main instrument to deal with such impacts was repetition and temporal diversification: *"Once, we had heavy rainfall with 40 litres [per m²] in 25 minutes, which partly washed away the soil at the slopes. The excavator re-located [the soil] and we re-sowed [these areas]"* (*LSPO5*; EN06). Droughts were another frequent obstacle, partly seen as an increasing problem due to climate change. In some cases, this lowered the possibility for farmers to forgo haymaking for plant material harvest: *"Many farmers tell us that they have less yield due to climate change. The hay is getting limited"* (*PFPO2*; EN03). Many practitioners reported lower species establishment due to drought after plant material transfer (EN05). In some cases, damages by wild boars, mice or deer occurred (EN01), but did not lead to the complete failure of restoration projects.

Resources

Limited resources were mentioned in relation to finances, personnel, and machinery. As a result, acquisition of these resources was sometimes time-consuming for the practitioners, and required a wide search radius.

Although insufficient financial resources were not frequently mentioned, some practitioners talked about such problems (RE04). However, external staff and suitable machines were hard to acquire in some regions. In terms of personnel, there were complaints of limited experience and dependence on farmers who have little time for restoration tasks: "*We have to find [farmers] who will engage in [plant material transfer], no one has experience. [...] If only one will not do the work, you have a problem, then the plant material lies around somewhere [waiting to be transferred]*" (*COAG2*; RE01). Lack of machinery was sometimes linked to the agricultural structure of a region: "*The first problem is that we are not a grassland region. [...] Therefore, there are no silage wagons*" (*AUTH8*; RE02). In such cases, more time had to be invested for acquisition, and the search radius often had to be extended: "*If [the farmer] does not have the proper loader wagon, you may have to acquire a contractor 70 km away... then it gets more complicated and expensive*" (*LSPO7*; RE02).

Project organization

While plant material transfer is, in principal, a simple method, the variety of tasks, short timeframes, and the different people involved make organization inherently challenging. Practitioners, thus, had to ensure good planning, task arrangement, and monitoring.

Timing was considered crucial in project organisation. Plant material transfer projects should be planned early in the eyes of many practitioners, which was not always realised (OR09). The complexity of plant material transfer projects, often with many involved people (OR6), requires good organization with close arrangement and communication (OR05). Combining tasks was suggested by several practitioners, particularly with respect to coordination: "*One person has to coordinate this. [...] In my eyes, good coordination is key [...], so that you can create the required conditions. When do you have access to the site, when is the farmer available for soil preparation, and so on*" (*LSPO1*; OR01). Accordingly, having own personnel was deemed beneficial (OR03). For dykes or road embankments, schedules determined by construction works increased the organizational challenge (OR10).

Practitioners often mentioned that monitoring practical tasks, e.g., by attending plant material harvest and application, was an important success factor (OR08). Several practitioners said that their projects were successful because they could implement their own ideas, while others criticised that decisions were taken from them: "*Sometimes we are now forced by the commissioner to use secondary donor sites. Then [the result] doesn't become so great, obviously*" (*LSCG1*; OR04).

Intrapersonal and interpersonal factors

Intrapersonal experience is the internal experience of an individual's mental and emotional processes, while interpersonal experience is the experience of an individual's interactions with other people. Practitioners underlined the relevance of both aspects for the outcomes of their restoration projects.

As an important intrapersonal factor, many practitioners mentioned the attitudes among the people involved in the restoration project. Openness towards the project idea was considered important, and disinterest strongly affected success of some restoration projects: "*The responsible person [in the commissioning company] had no interest in proper application [of the plant material], this was all done by the construction company. The sites were totally neglected [...], you almost don't want to look at them any longer*" (*LSPO5*; IF02). In contrast, enthusiasm and passion could be pivotal for successful outcomes (IF05). When technicians or farmers became interested in the projects, reliability increased greatly (IF06), and even motivated proactive involvement after longer collaboration: "*We have a contractor who is able to do things on his own by now [and] makes own proposals. This collaboration is the reason that many things work out very well [in our county]. In other regions, it's harder*" (*LSPO7*; IF03).

As a decisive interpersonal factor, getting familiar with each other and building trust with partners raised openness to the project ideas:

> "*We had farmers who [...] raised their hands and said 'No, we won't do [plant material transfer], that's too complicated for us!' They know that they have a conservation authority breathing down their necks. [...] For [plant material transfer], you need trust between conservation and agriculture. While you may build trust with something like this, trust is also a pre-condition for success*" (*AUTH7*; IF07).

Increased trust and experience levels reduced necessity of close-meshed monitoring and controlling: "*[This farmer] [...] knows why he does what he does. He's a lucky find. There are also other farmers with whom we cooperate, where we have to monitor a lot [more]*" (*AUTH9*; IF07, OR08, KE01, KE05). Building trust and acceptance was not only important concerning people directly involved in the restoration process, but also concerning farmers that manage sites: "*A good relationship with the farmers is important to us, so that the farmer knows what happens on his site, where the [plant] material is from and where it is applied*" (*AUTH1*; CU01, CU02).

Knowledge and experience

Knowledge and experience are considered crucial success factors. While practitioners were able to accelerate their learning by acquiring external information and support by experts, the ability to succeed reliably in plant material transfer appears only to grow with performing more projects. Many practitioners emphasised the importance of building on own experiences and knowledge over time:

> *"Reading some advice and thinking that you can just start now, it's not like this. Plant material transfer looks like a very simple method, and it is simple in principle. [...] Somehow learning it is quickly done. But if you want to get really good at it, it's very challenging. Then you need much experience... good practical, but also theoretical and botanical knowledge"* (*LSCG1*; KE03, KE05).

Less experienced practitioners often acquired external knowledge through exchange with experienced practitioners or scientists. In the best case, practitioners involved them in their projects: *"You need an expert who tells you when the time point [for harvest] is there, [...] otherwise the probability of failure is just too high"* (*AUTH1*; KE01).

Some practitioners considered monitoring of restored sites a key tool to learn from their own projects (KE06). Knowledge exchange between involved people and joint learning over time was mentioned several times as an important success factor (KE07). Local knowledge and regional networks were considered very helpful to achieve successful outcomes:

> *"I think if you have a good network in a region, if you know the donor sites and the farmers who can do the management [of the restored sites], [plant material transfer] is a very good method. If [landscape planning] offices work in a new region, it is a tedious task in the first year. Things depend on our experience and the trustful collaboration with [the implementers]"* (*LSPO7*; KE08).

Discussion and conclusions

The goal of our study is to contribute to improving practical grassland restoration outcomes with plant material transfer in the future. To achieve this, we have related relevant success factors from the practitioners' point of view to the existing scientific literature. We find many overlaps between scientific findings and practitioners’ views, but also remarkable research gaps (Table 4.1 gives an overview; see Table 4.S3 for the literature list, along with a detailed comparison of the practitioners’ views and the scientific findings, and Supplement 4.S1 for the method of literature search). In the following, we discuss our findings with regard to the four research questions (RQ) from the Introduction.

Table 4.1: Number of studies found in our literature review (total of 37 studies) considering the 17 success factor categories of plant material transfer identified in the practitioner interviews. For each category, the number of studies supporting or contradicting the practitioners’ views is given, along with the number of studies investigating further success factors unmentioned by the practitioners. See details on this comparison and the studies in Table 4.S3 and on the literature search methodology in Supplement 4.S1.

	Number of studies		
Category	**supportive**	**contradicting**	**success factors not mentioned**
Acquisition and choice of donor sites	7	0	3
Acquisition of restoration sites	0	0	1
Abiotic suitability of restoration sites	12	0	2
Previous use and state of restoration sites	3	0	0
Soil preparation	5	1	2
Harvest and transfer of plant material	6	0	3
Application of plant material	0	0	0
Additional measures	4	0	3
Transitional management	1	0	0
Practice of post-restoration management	3	0	1
Communication with post-restoration user	0	0	0
Financing of post-restoration management	0	0	0
Environmental events and weather conditions	3	0	0
Intrapersonal and interpersonal factors	0	0	0
Project organization	0	0	0
Resources	0	0	0

	Number of studies		
Category	**supportive**	**contradicting**	**success factors not mentioned**
Knowledge and experience	0	0	0

The scientific evidence supports the practitioners' views (RQ 1)

According to our literature review, science has almost exclusively investigated the rather process-related practical, technical, and ecological success factors of plant material transfer. Most prominently, scientific studies considered quality and composition of the donor sites (e.g., Kiehl et al., 2006; Wagner et al., 2021), abiotic conditions (e.g., Sengl et al., 2017; Sommer et al., 2023) and previous use of the restoration sites (e.g., Donath et al., 2007; Harvolk-Schöning et al., 2020), soil preparation (e.g., Bischoff et al., 2018; Szymura et al., 2022), plant material harvest (e.g., Bischoff et al., 2018; Kiehl et al., 2006), additional introduction of desired species (e.g., Hofmann et al., 2020; Slodowicz et al., 2023), and post-restoration management (Coiffait-Gombault et al., 2011; Rasran et al., 2007). Our analyses of the interviews show that all these aspects were considered relevant and mentioned frequently by the practitioners. Concerning the way these factors influence restoration success, there is a strong consensus between scientific findings and practitioners' views. For example, many practitioners underlined the importance of low nutrient supply of the restoration sites. This is supported by scientific studies where the panels of restored sites varied in nutrient richness (Schmiede et al., 2012; Sommer et al., 2023). However, some statements of the practitioners also indicate the existence of misleading narratives in practice. For example, LSCG1 reported attempts to develop low-productive meadows on pure gravel sites, which were unsuitable to support any meadow plant community due to very low nutrient supply (section "Abiotic suitability of restoration sites" of the Results).

Some questions investigated by our reviewed studies have not or barely been mentioned by the practitioners. For example, extensive research has been carried out on the optimal thickness of the plant material layer and the size ratio of the donor and restoration sites (e.g., Donath et al., 2006; Scotton, 2018), but the practitioners hardly mentioned this as a decisive success factor. It is likely that limitations such as the availability of donor sites and narrow time frames for plant material transfer and application do often times not allow for targeted decisions on the layer thickness. This is in accordance with some practitioners, such as Paul whose example we present in the introduction, mentioning limited availability of high-quality plant material as a problem. Generally, the layer thickness might just not be a crucial success factor in many cases, as the moisture-keeping effect only becomes relevant during droughts, and too thick layers only affect a subset of species, i.e., small-growing (Hansen et al., 2022) and small-seeded ones (Eckstein & Donath, 2005). Another success factor considered by science but not mentioned by practitioners was the removal of unwanted species on the restoration sites prior to plant material application (Hansen et al., 2022; Szymura et al., 2022). According to our interviews, in practice, such species were removed from restoration sites after plant material transfer as part of the transitional management. As overall, practitioners knew about the relevance of managing undesired species, this supports the conclusion that practitioners are generally aware of the important success factors as identified by science.

Many success factors are beyond the previous scope of science (RQ 2)

The different technical-ecological, process-related success factors considered by science and practitioners will, if taken into account, likely contribute to successful restoration outcomes in many cases. However, it has become evident that practitioners were only able to set up their projects accordingly if a range of additional conditions were met. Most prominently, trustful relationships between the involved people and good organization of tasks were key for many practitioners. The higher the practitioners' experience levels, the better they were able to take the different factors into account. For example, AUTH1 was aware of the importance of the right harvest date. However, they did not feel confident about defining it, but felt the need for an "expert" to do this (section "Knowledge and experience" of the Results).

Restoration science, mainly with regard to stakeholder relations in large-scale restoration projects, has identified the importance of good communication and trust-building (e.g., Druschke & Hychka, 2015; Gamborg et al., 2019; Strauser et al., 2020) and given advice on how to gain trust and foster interest and involvement of different stakeholders (Gornish et al., 2021). Most of the projects of the practitioners we interviewed were small-scale projects with one or few restoration sites. However, the importance of communicating and building trust with relevant stakeholders is also transferable to such small projects and can be facilitated by the smaller number of people involved (Metcalf et al., 2015). If practitioners can build on local networks, plant material transfer is more likely to succeed as key stakeholders do not have to be identified in advance. This aspect is also known from ecological restoration in other contexts (Buitenhuis & Dieperink, 2019; McGuire & Ehlinger, 2022). While trustful relationships can be helpful, organizing plant material transfer projects remains very challenging due to their inherent complexity, as pointed out by Latacz-Lohmann et al. (2022). Good organizational skills are therefore another key for practitioners, but will probably only grow with experience over time.

Knowledge acquisition and trust-building are key for practitioners (RQ 3)

Our findings indicate that the most promising bases for successful plant material transfer projects, such as good local networks and broad ecological and practical knowledge as well as organizational skills, will hardly ever be available to practitioners from the outset. Long-term restoration activities by established regional networks are therefore more promising compared to isolated short-term projects like Paul's, which is presented in the Introduction. We advise practitioners who have little or no experience with plant material transfer to level their expectations, be patient, and not to give up if initial restoration attempts are not successful. To improve chances of success, we recommend integrating experienced practitioners in restoration projects. When this is not possible, talking to experts and acquiring knowledge from compendiums may be the second-best option. Accordingly, we encourage expert practitioners of plant material transfer to share their knowledge and experiences.

In many cases, it will be crucial to collaborate with local farmers, authorities, and various other stakeholders. Practitioners must recognize the significance of cultivating positive and trustworthy relationships with these local partners. It is important to acknowledge that fostering trust and cultivating interpersonal connections requires deliberate effort and cannot be established instantaneously. By proactively convening different stakeholders and staff before commencing a project, a sense of community can be fostered, and potential sources of conflicts or mistrust can be identified. To achieve this objective, collaborative solutions can be developed to address specific concerns. For instance, during the process, it may become apparent that a farmer responsible for managing the site after restoration exhibits disinterest in the project and may consider re-sowing the area with commercial seeds, posing a risk to the restoration efforts. In such instances, strategies for appropriate management following the transfer of plant material to avoid weed dominance and improve acceptance can be openly discussed among stakeholders. Alternatively, if financial resources are available, a contractual arrangement might be explored to address this issue.

Interdisciplinary work and targeted communication are key for science (RQ 4)

Although scientific focus has primarily revolved around technical and ecological research pertaining to plant material transfer, recent studies have yielded novel and valuable insights in this domain such as into the transfer of invertebrates (Stöckli et al., 2021) or the long-term success factors of restoration (Harvolk-Schöning et al., 2020; Sommer et al., 2023). While some success factors examined by scientific research were not explicitly mentioned by practitioners, we encourage scientists to explore aspects that might extend beyond the immediate concerns of most practitioners. For example, the roles of functional connectivity provided by management (Klinger et al., 2021) or of soil organisms, such as earthworms (Buisson et al., 2021) or mycorrhizal fungi (Koziol et al., 2022), have rarely been investigated. Additionally, science could support practitioners by systematically investigating reasons for failure or success in restoration practice. As factors linked to project organization may strongly influence project outcomes, information on the interpersonal, intrapersonal, and organizational setups of the projects should be considered in addition to technical and ecological data. To this end, interdisciplinary studies of natural and social scientists on restoration success are needed. Further, science could support targeted spread of knowledge on plant material transfer by studying the distribution of practitioners' experience levels across regions and countries in Europe.

Our analysis did not provide a definitive answer regarding the specific means by which practitioners acquired their knowledge and formed their perspectives on success factors related to plant material transfer. Nevertheless, certain practices have shown promise in this regard. These include conducting literature reviews (e.g. Kiehl et al., 2010; Török et al., 2011), publishing compendiums and guidelines in national languages (e.g., Harnisch et al., 2014 and Hölzel, 2007 in German or Johansson et al., 1991 in Swedish), and organizing collaborative workshops with practitioners. Notably, the alignment between practitioners' views on success factors and the available scientific evidence suggests the effectiveness of these approaches. Generally, it is crucial that science communicates its results broadly using all these tools, potentially focusing on regions or countries where knowledge gaps are largest, once these have been identified.

Author contributions

Leonhard Sommer: Conceptualization, Methodology, Formal analysis, Investigation, Data Curation, Writing - Original Draft, Writing - Review & Editing, Visualization

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Acknowledgements

We thank the German Federal Environmental Foundation for funding the study. Our gratitude goes to the restoration practitioners who took the time to share their knowledge and experiences with us. We thank two reviewers for their valuable comments on two former versions of the manuscript. We also thank Björn Leineßer for his input on analysing the interviews.

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Supplementary materials

Supplement 4.S1: Approach of literature search for comparing the practitioners' views on success factors of grassland restoration with plant material transfer to the scientific evidence.

As this supplement has its own literature list, find it in the "Appendix A. Supplementary material", there named as Information A1, of the original research article:

Sommer, L., Castro Campos, B., Harvolk-Schöning, S., Donath, T. W., Kleinebecker, T., & Klinger, Y. P. (2023). Grassland restoration with plant material transfer – bridging the knowledge gap between science and practice. *Global Ecology and Conservation*, *47*, e02638. https://doi.org/10.1016/j.gecco.2023.e02638

Table 4.S1: Overview of the 33 interviewed practitioners, grouped by their fields of employment. For each practitioner, the way of involvement in their projects is marked by an “x” – in planning and organisation, realization of the measures, monitoring of the restored sites, or site use/ management after restoration. The same holds true for the types of habitats that were restored in the projects of the practitioners.

Partner	Planning	Realization	Monitoring	Post-restoration management	Wet grasslands	Floodplain grasslands	Mesic lowland grasslands	Mesic mountain grasslands	Acidic grasslands	Heathlands	Calcareous dry grasslands	Calcareous sandy grasslands
Authorities												
AUTH1	x				x		x					
AUTH2	x					x						
AUTH3	x					x						
AUTH4	x		x					x	x			
AUTH5	x					x						
AUTH6	x						x				x	
AUTH7	x					x						
AUTH8	x				x	x						
AUTH9	x											x
Compensation agencies												
COAG1	x	x			x		x			x		
COAG2	x					x						
Farms												
FARM1		x		x		x						
FARM2		x		x		x						
FARM3	x	x		x		x						
FARM4				x		x						
FARM5		x		x		x						x
Landscaping agencies												
LSCG1	x	x	x		x		x	x				
LSCG2	x	x				x	x				x	x
LSCG3		x					x		x			

Partner	**Planning**	**Realization**	**Monitoring**	**Post-restoration management**	**Wet grasslands**	**Floodplain grasslands**	**Mesic lowland grasslands**	**Mesic mountain grasslands**	**Acidic grasslands**	**Heathlands**	**Calcareous dry grasslands**	**Calcareous sandy grasslands**
Landscape planning offices												
LSPO1	x		x		x		x					
LSPO2	x				x		x					
LSPO3	x		x		x		x					
LSPO4	x		x		x		x					
LSPO5	x						x	x	x			
LSPO6	x		x		x		x			x		
LSPO7	x		x		x	x	x			x		x
Publicly funded project offices												
PFPO1	x					x						
PFPO2	x		x		x		x					
PFPO3	x		x		x		x					
PFPO4	x		x				x	x	x			
PFPO5	x	x	x								x	
PFPO6	x		x				x			x		
PFPO7	x		x				x		x			

Table 4.S2: Text segments from the interview transcripts of the 33 practitioners which were coded as success factors of plant material transfer, with the assigned success factors and their categories (sheet 1). Frequency of mentioning of the 17 success factor categories (sheet 2). Frequency of mentioning of the 173 success factor codes (sheet 3).

Due to the large format of this table, find it in the “Appendix A. Supplementary material”, there named as Table A2, of the original research article:

Sommer, L., Castro Campos, B., Harvolk-Schöning, S., Donath, T. W., Kleinebecker, T., & Klinger, Y. P. (2023). Grassland restoration with plant material transfer – bridging the knowledge gap between science and practice. *Global Ecology and Conservation*, *47*, e02638. https://doi.org/10.1016/j.gecco.2023.e02638

Table 4.S3: Comparison of the success factors of plant material transfer according to the practitioners and the respective scientific findings on these success factors according to our literature survey.

As this table has its own literature list, find it in the “Appendix A. Supplementary material”, there named as Table A3, of the original research article:

Sommer, L., Castro Campos, B., Harvolk-Schöning, S., Donath, T. W., Kleinebecker, T., & Klinger, Y. P. (2023). Grassland restoration with plant material transfer – bridging the knowledge gap between science and practice. *Global Ecology and Conservation*, *47*, e02638. https://doi.org/10.1016/j.gecco.2023.e02638

Abstract

Since the industrial revolution, land use changes and intensification of use have drastically reduced the area of species-rich, semi-natural grasslands in Central Europe. Active restoration of these ecosystems is therefore necessary and increasingly demanded by legislation. One method to (re-)introduce target plant species is the transfer of seed-containing plant material cut from species-rich, semi-natural donor sites. Given the urgency of the restoration task, the aim of this thesis is to contribute to understanding the success factors of this method, particularly in practice.

In a first study, 20 recipient sites of floodplain meadow restoration in Hesse, Germany, were revisited and investigated for vegetation composition in comparison to their corresponding donor sites 13-16 years after plant material transfer. To assess the potential for livestock feeding, biomass yield and energy contents were measured, too. In a second study, 41 recipient-donor site pairs from practical grassland restoration projects in different regions of Germany and Luxembourg spanning a broad moisture gradient were investigated. Vegetation was recorded, and soil analyses and information on restoration from the practice partners were used for success factor identification. In a third study, 33 practitioners of grassland restoration with plant material transfer were interviewed to compare their views on the topic to European scientific literature.

All three studies underline the critical importance of abiotic site conditions supporting the target plant communities. A frequent long-term problem is too high productivity of recipient sites, particularly in floodplain meadows. Site conditions, along with competition for the introduced plant species, are strongly dependent on the previous state of recipient sites. Raw soils, e.g., obtained by topsoil removal, provide low-competitive, nutrient-poor conditions, often enhancing restoration success. Generally, competition for the introduced species is lowered by adequate soil preparation, whose effect may, however, diminish over time. Harvest time for the plant material is decisive for the pool of transferable target species, and supplementing this pool by additional introduction methods, such as sowing, is useful. For maintenance of restored grassland communities, appropriate low-intensive post-restoration management is necessary. Sufficient biomass yield and energy content enable integration in feeding rations for livestock, buffering the costs of management. Practitioner interviews revealed that overarching factors such as project organisation, trust-building, and experience strongly influence how well the previously mentioned conditions can be met. To support grassland restoration in the coming decades, a challenge increased by climate change, intense knowledge exchange between science and practice and among practitioners is advised.

Zusammenfassung

Landnutzungsänderungen und die Intensivierung der Grünlandwirtschaft seit der Industrialisierung haben die Ausdehnung artenreichen, naturnahen Grünlands in Mitteleuropa drastisch reduziert. Daher ist eine aktive Wiederherstellung dieser Ökosysteme nötig, die auch gesetzlich zunehmend gefordert wird. Zielpflanzenarten können durch Übertragung samenreichen Mahdgutes von artenreichen, naturnahen Spenderflächen (wieder-)eingeführt werden. Angesichts der Dringlichkeit der Herausforderung soll diese Arbeit zum Verständnis der Erfolgsfaktoren bei dieser Methode besonders in der Praxis beitragen. Zunächst wurden 20 Empfängerflächen und die zugehörigen Spenderflächen am hessischen Oberrhein 13-16 Jahre nach Mahdgutübertragung wiederaufgesucht und die Vegetationszusammensetzung der Stromtalwiesen vergleichend erfasst. Zur Beurteilung des Futterwertes wurden zusätzlich Biomasseertrag und Energiegehalt der Aufwüchse bestimmt. In einer zweiten Studie wurden 41 Paare von Empfänger- und Spenderflächen mit unterschiedlicher Wasserversorgung aus Praxisprojekten in verschiedenen Regionen Deutschlands und Luxemburgs untersucht. Nach Vegetationserfassung wurden Bodenanalysen sowie Informationen von den Praxispartnerinnen und -partnern zur Identifizierung von Erfolgsfaktoren genutzt. In einer dritten Studie wurden 33 Praktikerinnen und Praktiker der Mahdgutübertragung befragt, um ihre Sicht auf die Thematik mit europäischen wissenschaftlichen Studien zu vergleichen. Alle drei Studien unterstreichen die Bedeutung geeigneter abiotischer Standortbedingungen für die Zielpflanzengesellschaften. Ein häufiges Langfristproblem sind zu produktive Empfängerflächen, besonders bei Stromtalwiesen. Die Standortbedingungen sowie die Konkurrenzsituation für eingebrachte Arten hängen stark vom Vorzustand der Flächen ab. Rohböden, die z.B. durch Oberbodenabtrag herstellbar sind, bieten konkurrenzarme und magere Bedingungen, was den Renaturierungserfolg oft steigert. Geeignete Bodenvorbereitung mindert die Konkurrenz für eingebrachte Arten, allerdings kann der Effekt über die Zeit nachlassen. Der Zeitpunkt der Mahdguternte bestimmt das Spektrum übertragbarer Arten, wobei eine Ergänzung dieses Artenpools z.B. durch zusätzliche Einsaaten sinnvoll ist. Zur Erhaltung der renaturierten Grünlandgesellschaften ist eine angepasste extensive Bewirtschaftung nötig. Ein hinreichendes Ertragsniveau sowie ein entsprechender Energiegehalt der Aufwüchse ermöglichen die Integration in Nutztierrationen, was die Pflegekosten abmildern kann. Die Praktikerinterviews haben gezeigt, dass übergreifende Erfolgsfaktoren wie die Projektorganisation, Vertrauensaufbau zwischen den Beteiligten sowie deren Erfahrungsniveau die Erfüllbarkeit der vorgenannten Bedingungen stark beeinflussen. Um die Grünlandrenaturierung in den kommenden Jahrzehnten zu unterstützen – eine durch den Klimawandel nochmals gewachsene Herausforderung – ist ein intensiver Wissenstransfer zwischen Wissenschaft und Praxis sowie innerhalb der Praxis anzuraten.

Acknowledgements

I am thankful to all people who contributed directly or indirectly to this dissertation. In particular, I want to express my gratitude to Dr. Sarah Harvolk-Schöning, to Prof. Dr. Till Kleinebecker, and to Prof. Dr. Tobias W. Donath for initiating the well-planned research project “Ziel erreicht?” on which the three studies were based, and for supervising my work. Furthermore, and very much, I am thankful to Dr. Yves P. Klinger, who took over my direct supervision during the project and who invested a lot of effort and time in enhancing the quality of my research methodology and of my scientific writing. You have contributed decisively to my personal and professional growth during the time of my dissertation project, Yves. I want to thank all other employees of the research group of Prof. Kleinebecker for being there and giving advice and mental support. Within the group staff, a particular thank you goes to Julia Höhl, Lukas Pabst, Joseph Scholz vom Hofe, and the research assistants without whom generation of our high-quality vegetation, soil, and biomass data would not have been possible. I am thankful to Ralf Schmiede for investing his free time to support me in determining the plant species over two field seasons, and to him and Matthias Harnisch for contributing information about the floodplain meadow project at the Northern Upper Rhine. Thanks to Dr. Simone Schneider and Dr. Bente Castro Campos for engaging as co-authors in one article each and to thereby improving the quality of this thesis. Finally, my gratitude goes to my parents, Astrid Sommer and Michael Sommer, to my sister, Henrike Sommer, and to my close friends for being my mental supporters over the whole timespan of this dissertation project.

Danksagung

Ich bin all jenen dankbar, die direkt oder indirekt zum Gelingen dieser Dissertation beigetragen haben. Im Besonderen möchte ich Dr. Sarah Harvolk-Schöning, Prof. Dr. Till Kleinebecker und Prof. Dr. Tobias W. Donath für ihre Betreuungsarbeit danken und dafür, dass sie das wirklich gut geplante Forschungsprojekt „Ziel erreicht?“ ins Leben gerufen haben, auf dem die drei Studien basierten. Weiterhin und in besonders hohem Maße bin ich Dr. Yves P. Klinger dankbar, der während der Projektlaufzeit meine Betreuung übernommen und eine Menge Zeit und Energie investiert hat, um die Qualität meiner Forschungsarbeit und meines wissenschaftlichen Schreibens zu verbessern. Du hast maßgeblich zu meinem Wachstum in persönlicher und fachlicher Hinsicht in der Zeit meiner Promotion beigetragen, Yves. Ich möchte allen weiteren Mitarbeiterinnen und Mitarbeitern der Arbeitsgruppe Kleinebecker danken, die auf verschiedene Weise mentale Unterstützung und fachlichen Rat geleistet haben. Innerhalb der Arbeitsgruppe geht ein besonderer Dank an Julia Höhl, Lukas Pabst, Joseph Scholz vom Hofe und an die wissenschaftlichen Hilfskräfte, ohne die die Gewinnung unserer hochwertigen Vegetations-, Boden- und Biomassedaten nicht möglich gewesen wäre. Ich bin weiterhin Ralf Schmiede dankbar, der seine Freizeit investiert hat, um mich über zwei Feldsaisons bei der Pflanzenbestimmung zu unterstützen, sowie ihm und Matthias Harnisch für die vielen Informationen rund um das Stromtalwiesenprojekt am hessischen Oberrhein. Danke zudem an Dr. Simone Schneider und Dr. Bente Castro Campos für ihr Engagement als Koautorinnen je eines Artikels und ihren damit verbundenen Beitrag zur Verbesserung der Qualität dieser Dissertation. Schließlich gilt mein besonderer Dank meinen Eltern, Michael und Astrid Sommer, meiner Schwester, Henrike Sommer, sowie meinen engen Freunden für ihre mentale Unterstützung über die gesamte Laufzeit der Promotion.

Versicherung gemäß Promotionsordnung des Fachbereichs

Ich erkläre: Ich habe die vorgelegte Dissertation selbständig und ohne unerlaubte fremde Hilfe und nur mit den Hilfen angefertigt, die ich in der Dissertation angegeben habe. Alle Textstellen, die wörtlich oder sinngemäß aus veröffentlichten Schriften entnommen sind, und alle Angaben, die auf mündlichen Auskünften beruhen, sind als solche kenntlich gemacht. Bei den von mir durchgeführten und in der Dissertation erwähnten Untersuchungen habe ich die Grundsätze guter wissenschaftlicher Praxis, wie sie in der „Satzung der Justus-Liebig-Universität Gießen zur Sicherung guter wissenschaftlicher Praxis“ niedergelegt sind, eingehalten.

Leonhard Sommer Gießen, 31.10.2025