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RESEARCH ARTICLE

Integrated assessment of grassland restoration methods across Germany: Direct harvesting and regional seed mixtures are most successful for vegetation outcomes

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Abstract

1. Restoring species-rich grasslands is one of the key tools to bend the biodiversity curve. However, so far there have been few landscape-scale assessments of restoration methods as applied by practitioners across many sites, soil conditions, and regions. To improve the effectiveness of grassland restoration, broad-scale standardised assessments are needed that incorporate both positive and negative references, and evaluate total plant diversity as well as characteristic grassland species.
2. The study assessed vascular plant diversity in 121 restored grasslands that cover different restoration methods, land-use legacies, restoration ages, and soil moisture levels across three regions in Germany. The results are compared with 33 positive (species-rich) and 33 negative (degraded) reference sites. We analysed diversity indices (total and characteristic plant species richness, total and characteristic Hill–Shannon diversity), the Favourable Conservation Status index (FCS_i), and the forb-graminoid ratio to assess the drivers and effects of restoration.
3. Restoration improved the diversity of vascular plant species compared with negative reference sites, and some restored grasslands reached the diversity and FCS_i levels of positive references. Active (re)introduction of species, such as direct harvesting methods and regional seed mixtures, was most successful in enhancing plant species diversity towards the target communities, while cultivar seed mixtures and management adaptation were less effective. Neither the previous land use nor the restoration age significantly affected the restoration outcome in terms of species richness and species composition.
4. *Synthesis and applications*. Direct harvesting and regional seed mixtures are the most effective methods to restore biodiverse and characteristic grassland plant communities. They outperform other methods regardless of land-use history and restoration age. This has positive implications for restoration of temperate

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grasslands in Central Europe, since land-use history is not a significant driver of restoration success, allowing the effective restoration on ex-arable land as well as on degraded grassland sites. Further studies should investigate the effects of combining direct harvesting and regional seed mixture sowing.

KEYWORDS
biodiversity, community assembly, forb-graminoid ratio, hay transfer, positive and negative reference site, restoration success, species diversity, UN Decade on Ecosystem Restoration

1 | INTRODUCTION

Species-rich grasslands harbour a large part of European vascular plant diversity, as they show some of the highest small-scale species richness worldwide (Habel et al., 2013; Wilson et al., 2012). These grasslands ensure important ecosystem functions and services such as pollination, carbon storage, and water conservation (Bengtsson et al., 2019; Lindborg et al., 2023), and they provide habitats for several other taxa including pollinators (Dengler et al., 2014; Wallis De Vries et al., 2007). Concurrently, species-rich grasslands are among the most endangered ecosystems in Europe and worldwide (European Commission et al., 2016; Newbold et al., 2015). Many grasslands have been converted into either cropland or forest or have been subject to intensified management due to fertilisation and sowing of productive cultivar species or abandonment, both leading to a poor conservation status (Dengler & Tischew, 2018; Wirth et al., 2024). Thus, the need for effective grassland restoration is high. A key question is, which restoration methods most successfully establish species-rich grasslands in terms of plant species diversity and functional composition.

In recent decades, promising methods of 'passive' and 'active' restoration have emerged to improve grassland restoration success (Atkinson & Bonser, 2020; Gann et al., 2019; Jones et al., 2018). Passive restoration is defined as a set of measures that terminate an ecosystem's degradation and allow ecosystem recovery (Jones et al., 2018). In grasslands, this approach implies improved management, for example, the reduction of fertiliser usage, low-intensity mowing or grazing, or the resumption of land use after abandonment. Passive restoration dispenses with active introduction of species, but seeks to achieve an adapted management ('management adaptation') and is therefore only applicable if the site harbours a viable soil seed bank of target species, or is embedded in a landscape with rich seed sources and functional dispersal pathways (Goret et al., 2021; Török et al., 2011). Otherwise, active restoration through the (re)introduction of desired vascular plant species is needed, for which various methods have been proposed (Slodowicz et al., 2023). Sowing seed mixtures has proven to be effective in establishing vascular plant species (Hedberg & Kotowski, 2010). However, while low-diversity seed mixtures (mainly comprising of strongly competitive cultivar varieties) can achieve high ground cover in the short term, they often lead to lower long-term diversity and are typically dominated by few perennial grasses (Ernst et al., 2025; Török et al., 2010). In contrast, high-diversity seed mixtures from regional sources more accurately reflect a typical community composition with a greater number of target species (Prach et al., 2021; Török et al., 2011) and tend to have higher establishment rates (Kiehl et al., 2010). If species-rich donor sites are available nearby, the transfer of directly harvested seed-containing material (hay or threshing material) can effectively establish the desired plant communities (Hedberg & Kotowski, 2010; Slodowicz et al., 2023).

So far, we know that restoration outcomes can vary depending on framework conditions such as land-use legacy, age, and site factors such as soil conditions and management (Brudvig et al., 2017; Grman et al., 2013), while integrated knowledge about successful restoration measures and management is still limited (Damschen et al., 2019; Lyons et al., 2023). Restoring species-rich grasslands takes time (Waldén & Lindborg, 2016), as community reassembly is a dynamic and slow process (Buisson et al., 2022). However, for the recovery of degraded ecosystems after restoration, this means the alignment with the values of (diversity) indices of the positive reference, can either be more or less complete or incomplete and sometimes it can slow down with time, because the final stage of ecosystem recovery is difficult to accomplish (Jones et al., 2018). Moreover, the type, intensity, and duration of degradation prior to restoration can play a crucial role for recovery success (Buisson et al., 2022). Successful restoration can be carried out on former arable land (Donath et al., 2007; Török et al., 2010) or on species-poor degraded grasslands (Baasch et al., 2016; Ernst et al., 2025), while the latter tends to be less successful (Donath et al., 2007; Kiehl et al., 2010). A clear understanding of the key drivers of restoration variation will improve its success and predictability (Brudvig & Catano, 2024).

Furthermore, quantitative goals with an acceptable range are necessary to assess restoration success (Brudvig & Catano, 2024). Integrated assessments of goal achievements are fostered by using multiple reference sites (Shackelford et al., 2024), or by comparing restored sites with both negative and positive references sites in terms of plant diversity (Wortley et al., 2013). Most commonly, 'positive reference' are used to analyse restoration success. However, comparisons with 'negative references', that is, degraded sites, can provide a more comprehensive and nuanced assessment of restoration success.

The assessment of restoration outcomes may differ considerably when a distinction is made between total and characteristic species richness for particular high nature value habitats. Evaluating restoration success solely based on total species richness can be misleading, since the total species richness might include opportunistic, ruderal, or invasive species that are not or less desired in the target community. Therefore, assessments of the ecological dynamics of grasslands must be based on the identification of all plant species and community specificity (characteristic species), as well as the forb-graminoid ratio (Nerlekar et al., 2024). Recently, integrated biodiversity metrics such as Hill numbers or Hill–Shannon analyses (Chao et al., 2014) open up new avenues for exploring restoration success from different perspectives of biodiversity outcomes. With the advent of coordinated European online flora databases (Chytrý et al., 2024), it has become easier to gain key information on characteristic grassland species (related to the EU Habitats Directive; see Mehtälä & Vuorisalo, 2007). Helm et al. (2015) distinguished between characteristic and derived ('non-habitat-specific') plant diversity to develop ecologically relevant metrics to assess management success and quantify the Favourable Conservation Status index (FCS_i), but this approach has rarely been applied in a landscape-scale approach.

Most grassland restoration studies focus on a single or a small number of sites and on a few habitat types within a limited geographical area, while systematic evaluations with a standardised monitoring procedure at the landscape-scale are rare (Brudvig et al., 2021; Grman et al., 2013). However, such broad-scale analyses of multiple real-world projects are essential to identify successful restoration methods and improve the replicability of restoration outcomes (Brudvig et al., 2017). This need is particularly pressing during the current UN Decade of Ecosystem Restoration, as well as in the context of the EU Nature Restoration Regulation, which demands efficient strategies to enable timely implementation of restoration projects (EU, 2024; UN, 2019).

Based on the knowledge gaps described above, we conducted a post-hoc assessment of restored grasslands sites along a gradient of soil moisture conditions in three regions across Germany. This study forms part of a large ecological and social-ecological research project on restoration success, entitled *Grassworks* (https://grassworksprojekt.de/en/), see Temperton et al. (2025) for details of the overall approaches and the applied methods. The sites represent diverse land-use legacies, restoration methods, and age since the main restoration intervention. We analysed total and characteristic grassland plant species richness and Hill–Shannon diversity, as well as assessing the effects of different factors on the forb-graminoid ratio and the index of Favourable Conservation Status (FCS_i; Helm et al., 2015). For this suite of response variables, we compared restored grasslands with positive and negative reference sites, asking the following questions: How do plant diversity and composition differ (i) between the restored sites compared with positive and negative references, and (ii) how are they affected by restoration methods, previous land use, and age of restoration? Additionally, we assessed the extent to which regional differences affect the outcomes.

2 | MATERIALS AND METHODS

2.1 | Study area and design

The present study is part of the *Grassworks* project (https://grassworksprojekt.de/en/), a large-scale research initiative focused on analysing ecological, socio-ecological, and economic aspects of grassland restoration in Germany (Temperton et al., 2025). We conducted the research in lowlands of northern, central and southern Germany, representing different geological and climatic conditions (Figure 1). In each region, we aimed to evaluate 40 restored sites complemented by at least ten positive reference sites (species-rich grasslands) and at least ten negative reference sites (degraded grasslands). Altogether, we assessed 121 restored sites and 33 sites of each reference type (187 sites in total). The sites covered a wide spectrum of soil moisture (dry, fresh, wet) and represent several common grassland types (dry: *Festuco-Brometea* or *Koelerio-Corynephoretea*; fresh: *Arrhenatheretalia elatioris*; wet: *Molinietalia caeruleae*; community names follow Leuschner & Ellenberg (2017) and Chytrý et al. (2024)). The grassland sites were restored either on former arable land or on degraded grassland and varied in the time since the main restoration intervention (2–36 years). All landowners have given their permit for us to assess their grassland sites at any time throughout the duration of the *Grassworks* project.

The sites were restored with different methods that fall into four categories: (i) direct harvesting, including the transfer of fresh plant material (hay or green hay) or threshing material from a nearby species-rich donor site to a receiver site; seeding was carried out either with a (ii) cultivar seed mixture, consisting of cultivated grasses and forbs, typically characterised by low species diversity and a small proportion of forb species, or (iii) with seed mixtures derived from certified wild seed propagation of regional provenance, that generally feature high species diversity (hereafter called 'regional seed mixture'). Finally, (iv) management adaptation, a 'passive' restoration approach without direct introduction of species, was selected, in which a site-specific adjustment of disturbance management was applied, for example, reintroduction of mowing or grazing on abandoned sites.

2.2 | Vegetation sampling

We conducted vegetation surveys in May or June 2022 or 2023, prior to the first mowing. A 200 m × 5 m transect (1000 m^2) was placed in a homogeneous part of each site and was partitioned into four 50-m sub-transects. In each sub-transect, we surveyed vegetation in a 2 m × 2 m plot. The four vegetation plots were combined for each site, so that all values refer to 16 m^2. We estimated the herb cover and the ratio of graminoids, forbs, and legumes. Herb cover can exceed 100% due to overlapping layers. We identified all vascular plants at the species level where possible and estimated their cover

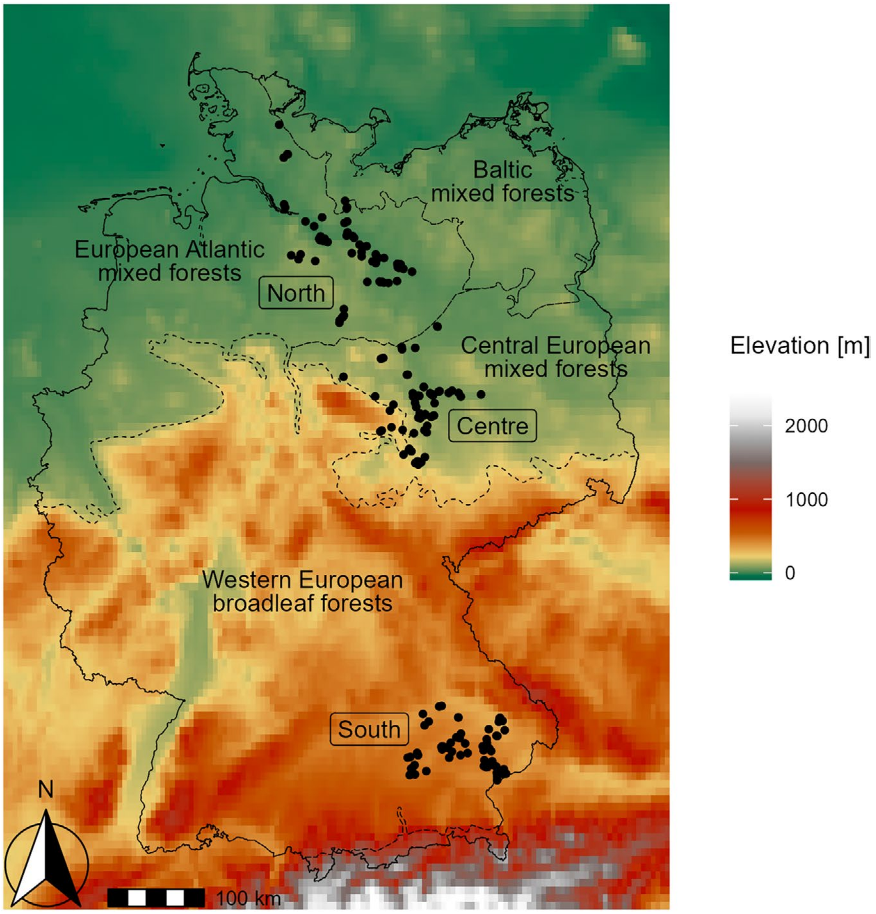

FIGURE 1 Location of restored grassland sites in northern, central, and southern Germany with some variation in altitude and continentality. Names of ecoregions *sensu* Dinerstein et al. (2017); for more details, see Temperton et al. (2025).

using an adapted Braun–Blanquet scale (Pfadenhauer et al., 1986) (Table S1). The nomenclature of the plants followed the German standard list (Buttler & Thieme, 2018; Jansen & Dengler, 2010, v1.5).

2.3 | Characteristic grassland species

We classified plants as either characteristic grassland species or non-grassland species (Table S5), using reference lists at both the European and national levels. At the European level, we used diagnostic species from all grassland habitats of the classification expert system EUNIS-ESy potentially occurring in the study area (Chytrý et al., 2020). At the national level, we classified species according to the German reference list of the European Habitats Directive (BfN, 2017) which includes phytosociological character and differentiating species, indicator species as well as common and constant species of grassland habitats. Since the Habitats Directive (BfN, 2017) does not encompass all wet grassland habitats, we included typical species of moist or wet mesotrophic to eutrophic hay meadow (R35, *Calthion palustris*; Chytrý et al., 2024) based on habitat lists from the German federal states of the three study regions (Brandt et al., 2023; LfU Bayern, 2022; LfU SH, 2023; MULE, 2020; NLWKN, 2011). All woody species were excluded from the analyses.

2.4 | Data analysis

2.4.1 | Data processing

All calculations and analyses were performed using R Statistical Software (v4.1.2, R Core Team, 2024). Individuals identified only at the family level ($n=2$) were removed to reduce possible double sampling of species. Those identified at the genus level were retained for analysis only if no species from the same genus were present at the same site; all others were also removed ($n=26$). To address sampling by multiple observers across three regions with varying species pool sizes, we converted species names to the aggregate level to minimise pseudo-turnover (Boch et al., 2022).

To quantify plant species diversity, we calculated the effective number of species (ENS), also called Hill numbers, with the aggregated species data using the package *hillR* (Li, 2018). We used numbers of order $q=0$, which is species richness, and of order $q=1$, which gives a stronger weight to common species in the community and is the exponential Shannon entropy (hereinafter referred to as Hill–Shannon diversity; Roswell et al., 2021), thus incorporating information about species evenness (Chao et al., 2014). The Hill–Shannon diversity was calculated for all plant species and for the subset of characteristic grassland species. We used for each species the mean cover of all four plots per site for calculating the Hill–Shannon diversity. We calculated the Favourable Conservation Status index (FCS_i) for each site, which is the natural logarithm of the ratio of the number of characteristic species to the number of derived (non-characteristic) species. FCS_i can be considered an indicator of biodiversity integrity and the status of biodiversity recovery and therefore as a measure of restoration success (Helm et al., 2015). As a measure of functional diversity, we calculated the forb-graminoid ratio by dividing mean estimated cover of the forb layer (including legumes) per site by the mean graminoid cover per site.

2.4.2 | Statistical analysis

We fitted generalised linear mixed models (GLMM) with the package *glmmTMB* (Brooks et al., 2017) to analyse the effects of restoration, as well as the drivers of restoration outcomes on various aspects of diversity, including total and characteristic species richness, total and characteristic Hill–Shannon diversity, forb-graminoid ratio and FCS_i. To determine the direct effect of restoration, we modelled the response of diversity variables to site type, that is, restored, positive or negative reference. Furthermore, we modelled the effects of different restoration methods (direct harvesting, regional seed mixture, cultivar seed mixture, management adaptation), previous land use (arable, grasslands), and age since the main restoration intervention (2–36 years). The distribution of data was checked, and an appropriate error distribution was chosen, that is, gamma distribution with log-link function for the Hill–Shannon diversity and forb-graminoid ratio, and a normal distribution for FCS_i. To account for overdispersion, we used a negative binomial error distribution for response variables that represent counts (species richness). The regions (north, centre, south) and soil moisture levels (dry, fresh, wet) were integrated as random factors in a crossed random intercept model. We found interactions between restoration age and random factors, but a random slope structure could be denied by AIC comparison.

In data exploration, the restoration method and the restoration age correlated significantly (ANOVA: $F_{3,104} = 19.1$, $p < 0.001$, $r^2 = 0.36$). The reason for this was the continued development of restoration methods over time, with the use of cultivar seed mixtures being predominant before 2010, and the development and more frequent use of other methods in the past approximately 15 years. However, to allow assessing the influence of restoration age on diversity, we created two models: (i) using only sites <20 years old ($n = 91$ sites) where collinearity is absent (ANOVA, $F_{3,87} = 2.13$, $p = 0.102$, $r^2 = 0.07$), and (ii) including the full dataset and excluding restoration age.

The assumptions of the model were checked by plotting residuals versus fitted values versus each covariate in the model, and versus each covariate not in the model (Zuur & Ieno, 2016). Where significant differences were recorded in the GLMMs, we conducted Tukey-adjusted pairwise comparisons of estimated marginal means (EMM) with the package *emmeans* (Lenth, 2024).

3 | RESULTS

3.1 | General findings

At the 187 study sites, we found 572 plant taxa, that is, genera, aggregates, sections, or species (here referred to as 'species'); 335 species were assigned as characteristic grassland plants (57%). Of the total species pool, 42% were found in the northern region (61 sites), 70% in the centre (66 sites), and 60% in the south (60 sites). Of the characteristic species pool ($n = 335$), 47% were found in the north, 74% in the centre and 66% in the south. On average, 37.0 ± 14.9 species and 30.5 ± 13.3 characteristic grassland species were sampled on 16 m^2 per site (combining four plots of a site; means ± SD). Generally, all vegetation parameters increased from north to south, while the values of the negative references were similar in all regions (Figures S1 and S2). Further, soil moisture levels showed a low influence on vegetation parameters, with the dry sites having higher total and characteristic species richness than moist and fresh sites (Figures S3 and S4). Forb cover was highest at positive references and sites restored with regional seed mixtures and direct harvesting (Figures S5 and S6). In contrast, graminoid cover was highest at negative references and sites restored with cultivar seed mixture (Figures S5 and S6).

3.2 | Restoration versus positive and negative references

In the GLMMs, all response variables significantly differed between the type of site (restored, positive or negative reference; Table 1; Figure 2). The response variables were significantly higher on restored or positive references than on negative references (Table S3). The total species richness, FCS_i, and the forb-graminoid ratio were similar in the restored sites and positive references (Figure 2a,e,f), while the characteristic species richness, total, and characteristic Hill–Shannon diversity were lower in the restored sites than in the positive references (Figure 2b–d; Table S3).

3.3 | Effects of restoration methods, previous land use, and age of restoration

Models with the reduced data set of sites younger than 20 years did not show an influence of restoration age on any of the response variables. In the full data set models (all restored sites, restoration age excluded), the restoration methods had a significant effect on all response variables (Table 2; Figure 3). Direct harvesting methods showed the highest values in all response variables, except for the forb-graminoid ratio, where the outcome of regional seed mixtures was higher but not significantly different from direct harvesting (Figure 3f; Table S4). The total species richness was even higher for direct harvesting than at positive reference sites. The forb-graminoid ratio in both direct harvesting and regional seed

TABLE 1 Results of the generalised linear mixed models comparing restored sites with reference sites (positive or negative) for different response variables (total and characteristic species richness, total and characteristic Hill–Shannon diversity, Index of Favourable Conservation Status (FCS_i) and forb-graminoid ratio).

	Total species richness		Char. Species richness		Total Hill–Shannon		Char. Hill–Shannon		FCS_i		Forb-graminoid ratio	
	Est ± SE	z	Est ± SE	z	Est ± SE	z	Est ± SE	z	Est ± SE	z	Est ± SE	z
(Intercept)	3.13 ± 0.13***	23.32	2.87 ± 0.15***	19.40	1.93 ± 0.19***	10.28	1.75 ± 0.19***	9.26	2.82 ± 0.15***	19.05	−1.25 ± 0.25***	−4.97
Restored sites	0.54 ± 0.06***	8.71	0.61 ± 0.06***	9.49	0.64 ± 0.08***	7.69	0.69 ± 0.08***	8.19	0.62 ± 0.06***	9.75	1.25 ± 0.17***	7.29
Positive reference	0.63 ± 0.07***	8.39	0.74 ± 0.08***	9.69	0.86 ± 0.10***	8.30	0.95 ± 0.10***	9.05	0.77 ± 0.08***	9.54	1.23 ± 0.21***	5.82
Region (random)	0.18		0.20		0.29		0.29		0.20		0.22	
Soil moisture (random)	0.11		0.12		0.08		0.08		0.12		0.27	
N	187		187		187		187		187		187	
R^2 marginal	0.28		0.32		0.23		0.26		0.29		0.26	
R^2 conditional	0.54		0.60		0.51		0.53		0.54		0.40	
AIC	1426		1358		1132		1086		132		309	

Note: Models follow the equation: Response ~ site type + (1|region) + (1|hydrology). Levels of significance: $^{*}p < 0.05$, $^{**}p < 0.01$, and $^{***}p < 0.001$. Region and hydrology are used as random factors in the models. Estimates on linear scale for FCS_i, all others on log scale. All variables relate to 16 m^2. Abbreviations: Est, model coefficient (estimate); SE, standard error; z, z-value.

mixture treatments was higher than in positive references (Figure 3; Table S4). The cultivar seed mixtures showed the lowest values in all response variables; only in FCS_i and the forb-graminoid ratio did it equal to management adaptation (Figure 3e,f; Figure 3; Table S4). None of the response variables differed significantly between direct harvesting and regional seed mixture (Figure 3a). Further, characteristic species richness, total and characteristic Hill–Shannon diversity, and FCS_i in direct harvesting and regional seed mixture differed from the cultivar seed mixture (Figure 3b–e; Table S4). The forb-graminoid ratio showed no differences in any of the restoration methods (Figure 3f). Management adaptation was not different from the cultivar and regional seed mixture for all response variables. Further, management adaptation showed lower numbers (for the total and characteristic species richness) and a lower FCS_i than direct harvesting (Figure 3a,b,e). In the other models, no difference to direct harvesting was detected (Table S4). FCS_i was the only variable where previous land use showed a significant difference, with sites that were already grassland before restoration reaching a higher index than those that were arable land (Table 2).

4 | DISCUSSION

4.1 | Restored diversity in comparison to positive and negative reference sites

The assessment of grassland restoration in the three regions showed that grassland restoration in Germany is generally successful, with total, characteristic and Hill–Shannon diversity, FCS_i, and forb-graminoid ratio reaching levels similar to positive reference sites. The species richness in restored sites was on average only 3.6 species lower and the characteristic species were only 4.6 lower than in positive references. In general, restored sites had far more species than negative references (+16.3 total, +14.7 characteristic plant species). We expected restored grasslands to have intermediate levels of plant species richness between negative and positive references, while restored sites were actually similar to positive references, but the higher variability in diversity metrics at restored compared with positive reference sites indicates a need for further investigation into the drivers of such variability. As the predictability of restoration measures and outcomes should be increased (*sensu* Brudvig et al., 2017), a better understanding of the mechanisms behind the higher variability found in restored grasslands is essential. However, supplementary factors such as soil preparation can have direct effects on restoration outcome (Schmiede et al., 2012) that go beyond an assessment of the primary restoration intervention. Our findings agree with several meta-analyses (Atkinson et al., 2022; Jones et al., 2018; Rey Benayas et al., 2009), with generally positive restoration outcomes without a full recovery in average, but a higher variability in restored versus positive references. Functional composition such as the forb-graminoid ratio is an important component of restoration outcome, along with species richness and composition. Eutrophication is one of the main drivers of biodiversity loss

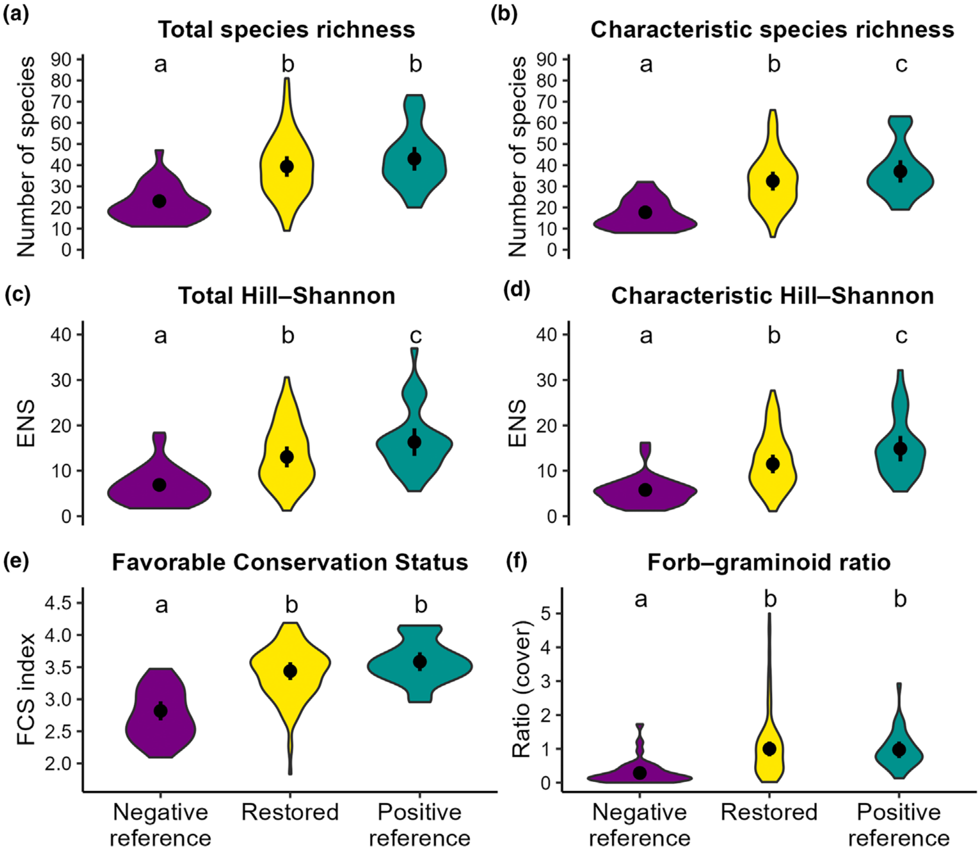

FIGURE 2 Effect of restoration on a suite of different diversity variables: (A) total plant species richness and (B) characteristic plant species richness (grasslands), (C) Hill–Shannon diversity based on total and (D) characteristic species and expressed as effective number of species (ENS), (E) Favourable Conservation Status index (FCS_i), and (F) forb-graminoid ratio compared with negative and positive reference sites. Black dots show estimated marginal means (EMM) and error bars show standard errors of model results. All values relate to 16 m^2 and show distribution density (frequency) of raw data in violin shapes. Different letters indicate significant differences ($p < 0.05$) based on Tukey-adjusted pairwise comparisons of EMMs.

in grasslands, as it leads to a predominance of grasses over forbs in terms of abundance rather than species richness (Nerlekar et al., 2024; Pywell et al., 2003). Interestingly, the grasslands across Germany in our study had similar forb-graminoid ratios as well as similar levels of FCS_i in restored compared with positive reference sites (Figure 2e,f).

Restored grasslands that harbour a higher number of rare species can take decades to reach species richness levels of ancient grasslands (Nerlekar & Veldman, 2020). Reasons usually given for lower species richness at restored sites can result from unsuccessful transfer of target species as well as establishment or persistence of non-target species (Shackelford et al., 2021). Additionally, suboptimal management can hamper reaching the desired outcomes (Tälle et al., 2018). Moreover, trajectories of restored sites depend on year effects such as weather conditions after seeding (Groves et al., 2020; Werner et al., 2020). Despite the multitude of different factors that can hinder the establishment of target species in restoration, in our study, restored sites had 9% fewer overall species than positive reference sites, which is in line with the meta-analysis by Atkinson et al. (2022), where restored sites had 13% less species than positive references.

In this context, it is important to note that although many restoration methods were successful, our data also showed considerable overlap between some restored and some negative references (some restored sites harboured considerably less plant species than some negative references as illustrated by overlapping violin plots in Figure 2), which in turn suggests the limited success or even failure of some interventions. However, we also found that the positive and negative reference sites overlapped partially. This finding suggests that the success of restoration measures is strongly context-dependent and might also relate to other factors such as soil seed bank or weather. Moreover, the issue of shifting biodiversity baselines needs to be taken into account, when assessing restoration success (Maron et al., 2021), since the positive references to which we compared the restoration sites may have lost characteristic species over time (see Temperton et al., 2025 for a discussion of this issue). Finally, the lower local species diversity can be linked to the size of the respective regional species pool (Zobel, 2016). In our study, this effect was expected and found, that is, the lower diversity of the northern sites is related to a latitudinal gradient of the German flora (cf. Finnie et al., 2007). In addition, even moderate land-use intensifications can worsen the diversity of positive reference sites over

TABLE 2 Results of the generalised linear mixed models testing effects of different restoration methods (restoration method, previous land use) for different response variables (total and characteristic species richness, total and characteristic Hill–Shannon diversity, Index of Favourable Conservation Status (FCS_i) and forb-graminoid ratio).

	Total species richness		Char. Species richness		Total Hill–Shannon		Char. Hill–Shannon		FCS_i		Forb-graminoid ratio	
	Est ± SE	z	Est ± SE	z	Est ± SE	z	Est ± SE	z	Est ± SE	z	Est ± SE	z
(Intercept)	3.43 ± 0.14***	25.27	3.23 ± 0.15***	21.28	2.26 ± 0.20***	11.10	2.14 ± 0.21***	10.12	3.19 ± 0.16***	20.13	−0.30 ± 0.31	−0.94
Management adaptation	0.12 ± 0.10	1.23	0.11 ± 0.10	1.09	0.32 ± 0.14*	2.35	0.31 ± 0.15*	2.11	0.09 ± 0.10	0.83	−0.16 ± 0.30	−0.53
Regional seed mixture	0.18 ± 0.07*	2.49	0.23 ± 0.07**	3.19	0.27 ± 0.10**	2.67	0.31 ± 0.11**	2.93	0.21 ± 0.08**	2.81	0.48 ± 0.23*	2.07
Direct harvesting	0.33 ± 0.08***	4.39	0.32 ± 0.08***	4.27	0.39 ± 0.11***	3.61	0.36 ± 0.11**	3.16	0.33 ± 0.08***	3.92	0.37 ± 0.23	1.60
Grassland	0.09 ± 0.05	1.69	0.10 ± 0.05	1.90	0.03 ± 0.08	0.41	0.03 ± 0.09	0.37	0.13 ± 0.06*	2.08	−0.02 ± 0.18	−0.14
Region (random)	0.18		0.20		0.31		0.31		0.21		0.17	
Hydrology (random)	0.10		0.13		0.08		0.12		0.13		0.41	
N	121		121		121		121		121		121	
R^2 marginal	0.14		0.13		0.08		0.07		0.12		0.09	
R^2 conditional	0.52		0.58		0.51		0.49		0.52		0.36	
AIC	914		868		727		710		59		252	

Note: Models follow the equation: Response ~ restoration method + previous land use + (1|region) + (1|hydrology). Levels of significance: *$p < 0.05$, **$p < 0.01$, and ***$p < 0.001$. Region and hydrology are used as random factors in the models. Estimates on linear scale for FCSi, all others on log scale. Values all relate to 16 m^2. Abbreviations: Est, model coefficient (estimate); SE, standard error; z, z-value.

time (Gossner et al., 2016). This in turn can negatively affect species dispersal processes from neighbouring species-rich sites (Buisson et al., 2022; Conradi et al., 2017a; Dellicour et al., 2023).

4.2 | Influence of restoration methods

Our study compared different methods commonly used in grassland restoration across Germany and clearly found that some methods performed better than others in restoring vegetation parameters, with the transfer of directly harvested material and the use of regional seed mixtures being most successful in restoring total and characteristic species richness and habitat integrity, compared with cultivar seed mixtures and management adaptation. Based on these findings, we recommend direct harvesting and sowing of regionally adapted seed mixtures for grassland restoration. However, key logistical requirements must be considered, such as the availability of species-rich donor sites close to the receptor site, commercial supply of regional wild seeds from certified regional propagation, and access to suitable machinery for implementation (Goret et al., 2021; Török et al., 2010). For practical applications, combining restoration interventions, for example, direct harvesting with sowing of regional seed mixtures, is also advisable, as this can increase restoration success (Baasch et al., 2016). The regional seed mixtures should be locally adapted not only by species selection but also by a trait-based design of the seed mixtures (Coutinho et al., 2023; Laughlin et al., 2018). In addition, landscape conditions should be considered in restoration projects, as target plant species can colonise the restored site if they are still abundant in the landscape (Johanidesová et al., 2015; Prach et al., 2015). Although the regional seed mixture performed similarly to the cultivar seed mixture and management adaptation in terms of total species richness, it outperformed the cultivar seed mixtures in establishing characteristic grassland species. Clearly, sowing cultivar mixtures was less successful for establishing characteristic grassland species than total plant species richness. We generally found that management adaptation had similar effects to regional seed mixture sowing, performing only slightly worse than regional seed mixtures. These results are in line with a meta-analysis of 13 grassland restoration studies across Europe (Slodowicz et al., 2023) where the seed source explained a significant amount of variation in plant species richness, with the addition of seeds from a species-rich donor site being the most successful approach. Kiehl et al. (2010) also clearly underlined the direct and lasting success of green hay transfer. Additionally, studies have shown that management adaptation is an appropriate restoration method in some cases (Török et al., 2011), and is the first choice when grasslands suffer from shrub encroachment and litter accumulation, but characteristic species are still present, albeit in small populations (Köhler et al., 2023). Therefore, the key component that guarantees successful restoration of desired vegetation communities after management adaptation is the species inventory and the availability of seeds in the landscape and/or at the site (Goret et al., 2021; Török et al., 2011).

Although sowing of cultivar seed mixtures produced similar results to management adaptation for all vegetation characteristics,

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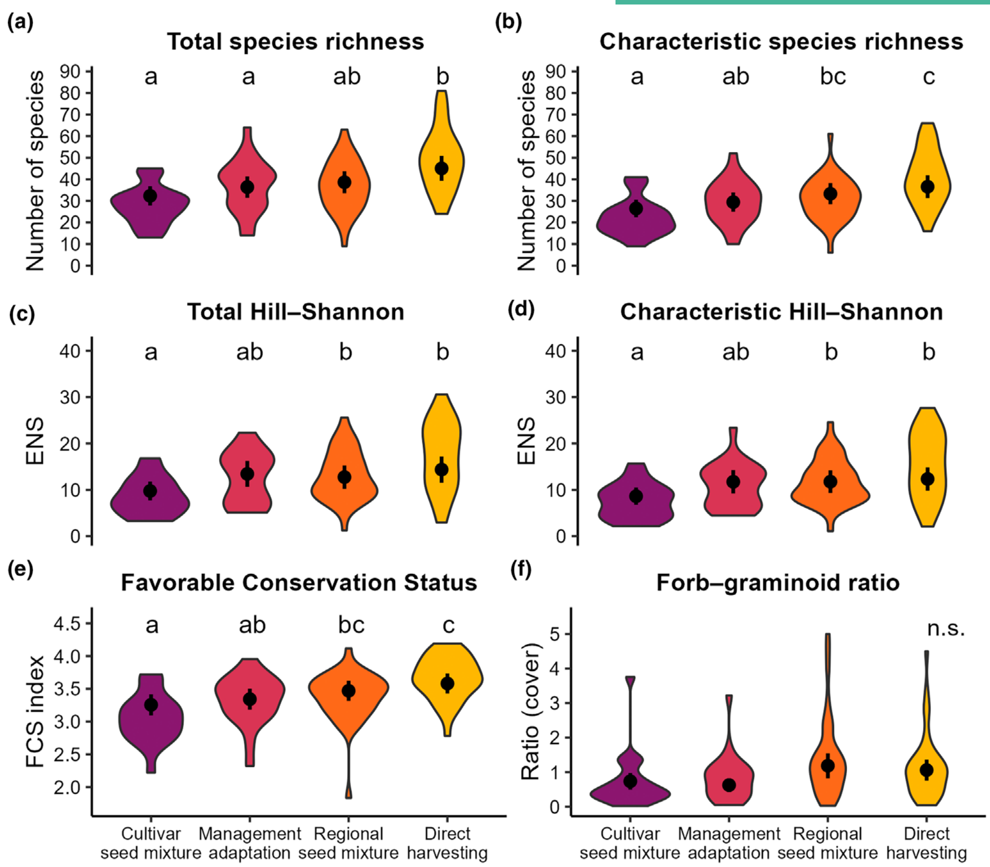

FIGURE 3 Effect of different restoration methods on (A) total and (B) characteristic species richness, (C) Hill–Shannon diversity based on total, and (D) characteristic species expressed as effective number of species (ENS), (E) the Index of Favourable Conservation Status index (FCS_i), and (F) forb-graminoid ratio. All variables relate to 16 m^2. Black dots show estimated marginal means (EMM) and error bars show standard errors of model results. Distribution density (frequency) of raw data in violin shapes. Different letters indicate significant differences ($p < 0.05$) based on Tukey-adjusted pairwise comparisons of EMMs.

the spread of data points was generally skewed towards lower values (Figure 3). Sowing cultivar seed mixtures has been common practice, particularly prior to the past decade (Kiehl et al., 2010), but is inappropriate for restoring species-rich grasslands (Conrad & Tischew, 2011; Goret et al., 2021; Kirmer et al., 2012), because cultivar seed mixtures are often species-poor and consist mostly of grass species and a few dominant forb species. Cultivar seed mixtures therefore usually lead to species-poor grasslands that are dominated by common grasses (Ernst et al., 2025; Török et al., 2010) and harbour the risk of outcompeting the local genotypes through a higher fitness of the introduced cultivar genotypes (Vander Mijnsbrugge et al., 2010). As a consequence, the introduction of species can lead to a temporary establishment advantage through priority effects through early establishment success (*sensu* Von Gillhaussen et al., 2014), which often results in uniform plant communities dominated by introduced grass cultivars when cultivar seed mixtures are sown (Conrad & Tischew, 2011). Further, cultivar species do not support higher trophic levels as effectively as regionally adapted genotypes: Bucharova et al. (2022) showed that provenance identity affected flower–pollinator interactions and interacting insect diversity. Therefore, species introduction measures need to consider the origin of seeds and the number, variety, and share of species that are typical of a respective site.

Surprisingly, all restoration methods in our study reached a similar forb-graminoid ratio, which is considered a significant indicator of vegetation structure and needs clear promotion in grassland restoration (Nerlekar et al., 2024) as it directly benefits biodiversity at higher trophic levels and ecosystem multifunctionality (Curtis et al., 2015; Tobisch et al., 2023). The relatively low variability between restoration methods regarding the forb-graminoid ratio is encouraging, but the ratio of forbs to graminoids was generally rather low at all study sites, with negative references showing the lowest values. Studies covering changes in forb-graminoid ratios remain rare, but anecdotal evidence points towards higher forb-graminoid ratios in the past, likely influenced by eutrophication (Schüle et al., 2023). As the forb-graminoid ratio in the existing vegetation is not only affected by the number of forb species in seed mixtures, but also by their proportion in the total weight of the seed mixtures, this proportion must be taken into account when planning grassland restoration. Seed mixtures often show a high proportion of grass species, even if they are species-rich and native (own observations with available mixtures from regional seed company mixtures).

Interestingly, previous land use, cropland or grassland, had no significant effect on restoration outcomes, with the exception that previous grassland use led to an increased conservation status (FCS_i)

compared with converted arable land. Several recent meta-analyses underline key effects of management change (Schils et al., 2022; Schüle et al., 2023) on plant diversity, rather than direct effects of major land-use change like from cropland to grassland. It seems that any legacy of fertilisation on previous cropland is not clearly detectable in our assessment across Germany, except only for the FCS_i, which was significantly negatively influenced by previous cropping land use.

The time since the main restoration intervention also had no significant impact on the restoration outcome. A possible simple explanation could be that contrasting trajectories among sites (for example, the increase in species richness in some sites and the decrease of species in others) masked the age effect of restored sites. However, this finding is rather surprising, as some studies have shown that vegetation composition in grassland restoration can be positively influenced by time since restoration (Noreika et al., 2020; Waldén & Lindborg, 2016; but see Atkinson et al., 2022). However, our findings are consistent with those of Slodowicz et al. (2023), who also showed that mainly the quality and origin of introduced species, but not other factors such as previous land use, restoration age, and seed bed preparation, influenced restoration outcomes. The lack of a temporal trend in our study might also indicate that initial establishment is the main driver of longer-term plant diversity patterns, with little further accumulation of species over time, thus suggesting a possible role for priority effects (Weidlich et al., 2021) or the importance of niches being available during the arrival phase, especially in more mesic conditions (Conradi et al., 2017b).

5 | CONCLUSION

Grassland ecosystems, despite their high biodiversity and essential ecosystem functions, continue to decline in extent and quality, highlighting the urgent need for effective restoration. Our results demonstrate that restored grasslands under dry, mesic, or moist conditions can match the ecological quality of species-rich reference sites, with restoration outcomes strongly influenced by the method applied. The four restoration approaches tested, that is, management adaptation, sowing of cultivar or regional seed mixtures, or directly harvested material, produce vegetation outcomes spanning the full gradient from still degraded to target conditions. Active (re) introduction of target species is a main driver of restoration success, with direct harvesting and regional seed mixtures producing the best outcomes. On the contrary, previous land use influences the Favourable Conservation Status but no other parameters, and restoration age does not affect vegetation outcomes. The forb-graminoid ratio is slightly higher in restored compared with negative reference sites. Thus, practitioners should focus on the (re)introduction of characteristic grassland species, in particular on increasing the forb-graminoid ratio, either by using species-rich material from direct harvesting or species-rich regional seed mixtures to secure successful and long-term sustainable grassland restoration. Further studies should primarily investigate conditions and approaches under which combining different restoration interventions could increase restoration success, particularly when considering the still ongoing decline of grassland biodiversity. Combining direct harvesting with sowing of target plant species is particularly useful if, for example, only inferior quality donor sites are available in the surrounding or if the optimal time for seed harvesting has been missed. However, combinations of management adaptation and additional introduction of missing target species could also increase the probability for successful grassland restoration.

AUTHOR CONTRIBUTIONS

Anita Kirmer, Johannes Kollmann, Jacqueline Loos, Vicky M. Temperton, and Sabine Tischew conceived the *Grassworks* project. Anita Kirmer, Johannes Kollmann, Christin Juno Laschke, Annika Schmidt, Line Sturm, Vicky M. Temperton, Alina Twerski, and Miriam Wiesmeier designed the standardised vegetation surveys across the three regions. Christin Juno Laschke, Annika Schmidt, Line Sturm, Alina Twerski, and Miriam Wiesmeier mainly conducted the fieldwork with additional support from Werner Härdtle. Christin Juno Laschke analysed the data. Christin Juno Laschke, Alina Twerski, and Markus Bauer mainly wrote the manuscript with additional support from Johannes Kollmann, Jacqueline Loos, and Vicky M. Temperton, while all authors revised and approved the final version.

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CONFLICT OF INTEREST STATEMENT

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

DATA AVAILABILITY STATEMENT

Processed data and R scripts are published in Zenodo: https://doi.org/10.5281/zenodo.18621272 (Laschke et al., 2026). Raw data is available from the Pangaea Repository (Felden et al., 2023): https://doi.org/10.1594/PANGAEA.993406 (Twerski et al., 2026a) and https://doi.org/10.1594/PANGAEA.993401 (Twerski et al., 2026b).

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REFERENCES

Atkinson, J., & Bonser, S. P. (2020). "Active" and "passive" ecological restoration strategies in meta-analysis. *Restoration Ecology*, *28*(5), 1032–1035. https://doi.org/10.1111/rec.13229

Atkinson, J., Brudvig, L. A., Mallen-Cooper, M., Nakagawa, S., Moles, A. T., & Bonser, S. P. (2022). Terrestrial ecosystem restoration increases biodiversity and reduces its variability, but not to reference levels: A global meta-analysis. *Ecology Letters*, *25*(7), 1725–1737. https://doi.org/10.1111/ele.14025

Baasch, A., Engst, K., Schmiede, R., May, K., & Tischew, S. (2016). Enhancing success in grassland restoration by adding regionally propagated target species. *Ecological Engineering*, *94*, 583–591. https://doi.org/10.1016/j.ecoleng.2016.06.062

Bengtsson, J., Bullock, J. M., Egoh, B., Everson, C., Everson, T., O'Connor, T., O'farrell, P. J., Smith, H. G., & Lindborg, R. (2019). Grasslands—More important for ecosystem services than you might think. *Ecosphere*, *10*(2), e02582. https://doi.org/10.1002/ecs2.2582

BfN. (2017). *Lebensraumtypen nach Anhang I der FFH-Richtlinie: (mit Ausnahme der marinen und Küstenlebensräume) (Stand: Oktober 2017). BfN-Skripten* (Vol. *481*). Bundesamt für Naturschutz. https://doi.org/10.19217/skr481

Boch, S., Küchler, H., Küchler, M., Bedolla, A., Ecker, K. T., Graf, U. H., Moser, T., Holderegger, R., & Bergamini, A. (2022). Observer-driven pseudoturnover in vegetation monitoring is context-dependent but does not affect ecological inference. *Applied Vegetation Science*, *25*(3), e12669. https://doi.org/10.1111/avsc.12669

Brandt, I., Hastedt, J., & Haacks, M. (2023). *Kartieranleitung und Biotoptypenschlüssel für die Biotopkartierung in Hamburg: einschließlich der Definitionen besonders geschützter Biotope nach §*. Behörde für Umwelt, Klima, Energie und Agrarwirtschaft.

Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Mächler, M., & Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, *9*(2), 378–400. https://doi.org/10.32614/RJ-2017-066

Brudvig, L. A., Barak, R. S., Bauer, J. T., Caughlin, T. T., Laughlin, D. C., Larios, L., Matthews, J. W., Stuble, K. L., Turley, N. E., & Zirbel, C. R. (2017). Interpreting variation to advance predictive restoration science. *Journal of Applied Ecology*, *54*(4), 1018–1027. https://doi.org/10.1111/1365-2664.12938

Brudvig, L. A., & Catano, C. P. (2024). Prediction and uncertainty in restoration science. *Restoration Ecology*, *32*(8), e13380. https://doi.org/10.1111/rec.13380

Brudvig, L. A., Turley, N. E., Bartel, S. L., Bell-Dereske, L., Breland, S., Damschen, E. I., Evans, S. E., Gibbs, J., Hahn, P. G., Isaacs, R., Ledvina, J. A., Orrock, J. L., Sorenson, Q. M., & Stuhler, J. D. (2021). Large ecosystem-scale effects of restoration fail to mitigate impacts of land-use legacies in longleaf pine savannas. *Proceedings of the National Academy of Sciences of the United States of America*, *118*(17), e2020935118. https://doi.org/10.1073/pnas.2020935118

Bucharova, A., Lampei, C., Conrady, M., May, E., Matheja, J., Meyer, M., & Ott, D. (2022). Plant provenance affects pollinator network: Implications for ecological restoration. *Journal of Applied Ecology*, *59*(2), 373–383.

Buisson, E., Archibald, S., Fidelis, A., & Suding, K. N. (2022). Ancient grasslands guide ambitious goals in grassland restoration. *Science*, *377*(6606), 594–598. https://doi.org/10.1126/science.abo4605

Buttler, K. P., & Thieme, M. (2018). Florenliste von Deutschland—Gefäßpflanzen. Version 10 (August 2018): Archivierte Fassung als PDF-Datei. https://doi.org/10.11585/buttler_et_al_florenliste_v10

Chao, A., Chiu, C.-H., & Jost, L. (2014). Unifying species diversity, phylogenetic diversity, functional diversity, and related similarity and differentiation measures through Hill numbers. *Annual Review of Ecology, Evolution, and Systematics*, *45*(1), 297–324. https://doi.org/10.1146/annurev-ecolsys-120213-091540

Chytrý, M., Řezníčková, M., Novotný, P., Holubová, D., Preislerová, Z., Attorre, F., Biurrun, I., Blažek, P., Bonari, G., Borovyk, D., Čeplová, N., Danihelka, J., Davydov, D., Dřevojan, P., Fahs, N., Guarino, R., Güler, B., Hennekens, S. M., Hrivnák, R., … Axmanová, I. (2024). FloraVeg.EU — An online database of European vegetation, habitats and flora. *Applied Vegetation Science*, *27*(3), e12798. https://doi.org/10.1111/avsc.12798

Chytrý, M., Tichý, L., Hennekens, S. M., Knollová, I., Janssen, J. A. M., Rodwell, J. S., Peterka, T., Marcenò, C., Landucci, F., Danihelka, J., Hájek, M., Dengler, J., Novák, P., Zukal, D., Jiménez-Alfaro, B., Mucina, L., Abdulhak, S., Aćić, S., Agrillo, E., … Schaminée, J. H. J. (2020). Eunis habitat classification: Expert system, characteristic species combinations and distribution maps of European habitats. *Applied Vegetation Science*, *23*(4), 648–675. https://doi.org/10.1111/avsc.12519

Conrad, M. K., & Tischew, S. (2011). Grassland restoration in practice: Do we achieve the targets? A case study from Saxony-Anhalt/Germany. *Ecological Engineering*, *37*(8), 1149–1157. https://doi.org/10.1016/j.ecoleng.2011.02.010

Conradi, T., Temperton, V. M., & Kollmann, J. (2017a). Beta diversity of plant species in human-transformed landscapes: Control of community assembly by regional productivity and historical connectivity. *Perspectives in Plant Ecology, Evolution and Systematics*, *24*, 1–10. https://doi.org/10.1016/j.ppees.2016.10.001

Conradi, T., Temperton, V. M., & Kollmann, J. (2017b). Resource availability determines the importance of niche-based versus stochastic community assembly in grasslands. *Oikos*, *126*(8), 1134–1141. https://doi.org/10.1111/oik.03969

Coutinho, A. G., Carlucci, M. B., & Cianciaruso, M. V. (2023). A framework to apply trait-based ecological restoration at large scales. *Journal of Applied Ecology*, *60*(8), 1562–1571.

Curtis, R. J., Brereton, T. M., Dennis, R. L. H., Carbone, C., & Isaac, N. J. B. (2015). Butterfly abundance is determined by food availability and is mediated by species traits. *Journal of Applied Ecology*, *52*(6), 1676–1684. https://doi.org/10.1111/1365-2664.12523

Damschen, E. I., Brudvig, L. A., Burt, M. A., Fletcher, R. J., Haddad, N. M., Levey, D. J., Orrock, J. L., Resasco, J., & Tewksbury, J. J. (2019). Ongoing accumulation of plant diversity through habitat connectivity in an 18-year experiment. *Science*, *365*(6460), 1478–1480. https://doi.org/10.1126/science.aax8992

Dellicour, M., Goret, T., Piqueray, J., Fayolle, A., Bindelle, J., & Mahy, G. (2023). Success of passive and active restoration of lowland hay meadows with regard to current and historical references. *Frontiers in Ecology and Evolution*, *11*, 1136206. https://doi.org/10.3389/fevo.2023.1136206

Dengler, J., Janišová, M., Török, P., & Wellstein, C. (2014). Biodiversity of Palaearctic grasslands: A synthesis. *Agriculture, Ecosystems & Environment*, *182*, 1–14. https://doi.org/10.1016/j.agee.2013.12.015

Dengler, J., & Tischew, S. (2018). Grasslands of Western and northern Europe-between. *Grasslands of the World: Diversity, Management and Conservation*, 27–63.

Dinerstein, E., Olson, D., Joshi, A., Vynne, C., Burgess, N. D., Wikramanayake, E., Hahn, N., Palminteri, S., Hedao, P., Noss, R., Hansen, M., Locke, H., Ellis, E. C., Jones, B., Barber, C. V., Hayes, R., Kormos, C., Martin, V., Crist, E., … Saleem, M. (2017). An ecoregion-based approach to protecting half the terrestrial realm. *Bioscience*, *67*(6), 534–545. https://doi.org/10.1093/biosci/bix014

Donath, T. W., Bissels, S., Hölzel, N., & Otte, A. (2007). Large scale application of diaspore transfer with plant material in restoration practice—Impact of seed and microsite limitation. *Biological Conservation*, *138*(1–2), 224–234. https://doi.org/10.1016/j.biocon.2007.04.020

Ernst, L. M., Thiele, J., Dieker, P., Temperton, V. M., & Dauber, J. (2025). Biodiversity on old permanent vs. restored grassland is driven by small-scale land-use intensity and habitat connectivity. *Restoration Ecology*, *33*, e70029. https://doi.org/10.1111/rec.70029

EU. (2024). Regulation (EU) 2024/1991 of the European Parliament and of the Council of 24 June 2024 on nature restoration and amending Regulation (EU) 2022/869.

European Commission (2016). *Directorate-General for Environment, European red list of habitats. Part 2, Terrestrial and freshwater habitats*. Publications Office. https://data.europa.eu/doi/10.2779/091372

Felden, J., Möller, L., Schindler, U., Huber, R., Schumacher, S., Koppe, R., Diepenbroek, M., & Glöckner, F. O. (2023). PANGAEA—Data Publisher for earth & environmental science. *Scientific Data*, *10*(1), 347. https://doi.org/10.1038/s41597-023-02269-x

Finnie, T. J. R., Preston, C. D., Hill, M. O., Uotila, P., & Crawley, M. J. (2007). Floristic elements in European vascular plants: An analysis based on atlas florae Europaeae. *Journal of Biogeography*, *34*(11), 1848–1872. https://doi.org/10.1111/j.1365-2699.2007.01750.x

Gann, G. D., McDonald, T., Walder, B., Aronson, J., Nelson, C. R., Jonson, J., Hallett, J. G., Eisenberg, C., Guariguata, M. R., Liu, J., Hua, F., Echeverria, C., Gonzales, E., Shaw, N., Decleer, K., & Dixon, K. W. (2019). International principles and standards for the practice of ecological restoration. Second edition. *Restoration Ecology*, *27*, S1–S46. https://doi.org/10.1111/rec.13035

Goret, T., Janssens, X., & Godefroid, S. (2021). A decision-making tool for restoring lowland grasslands in Europe. *Journal for Nature Conservation*, *63*, 126046. https://doi.org/10.1016/j.jnc.2021.126046

Gossner, M. M., Lewinsohn, T. M., Kahl, T., Grassein, F., Boch, S., Prati, D., Birkhofer, K., Renner, S. C., Sikorski, J., Wubet, T., Arndt, H., Baumgartner, V., Blaser, S., Blüthgen, N., Börschig, C., Buscot, F., Diekötter, T., Jorge, L. R., Jung, K., … Allan, E. (2016). Land-use intensification causes multitrophic homogenization of grassland communities. *Nature*, *540*(7632), 266–269. https://doi.org/10.1038/nature20575

Grman, E., Bassett, T., & Brudvig, L. A. (2013). Editor'S CHOICE: Confronting contingency in restoration: Management and site history determine outcomes of assembling prairies, but site characteristics and landscape context have little effect. *Journal of Applied Ecology*, *50*(5), 1234–1243. https://doi.org/10.1111/1365-2664.12135

Groves, A. M., Bauer, J. T., & Brudvig, L. A. (2020). Lasting signature of planting year weather on restored grasslands. *Scientific Reports*, *10*(1), 5953. https://doi.org/10.1038/s41598-020-62123-7

Habel, J. C., Dengler, J., Janišová, M., Török, P., Wellstein, C., & Wiezik, M. (2013). European grassland ecosystems: Threatened hotspots of biodiversity. *Biodiversity and Conservation*, *22*(10), 2131–2138. https://doi.org/10.1007/s10531-013-0537-x

Hedberg, P., & Kotowski, W. (2010). New nature by sowing? The current state of species introduction in grassland restoration, and the road ahead. *Journal for Nature Conservation*, *18*(4), 304–308. https://doi.org/10.1016/j.jnc.2010.01.003

Helm, A., Zobel, M., Moles, A. T., Szava-Kovats, R., & Pärtel, M. (2015). Characteristic and derived diversity: Implementing the species pool concept to quantify conservation condition of habitats. *Diversity and Distributions*, *21*(6), 711–721. https://doi.org/10.1111/ddi.12285

Jansen, F., & Dengler, J. (2010). Plant names in vegetation databases — A neglected source of bias. *Journal of Vegetation Science*, *21*(6), 1179–1186.

Johanidesová, E., Fajmon, K., Jongepierová, I., & Prach, K. (2015). Spontaneous colonization of restored dry grasslands by target species: Restoration proceeds beyond sowing regional seed mixtures. *Grass and Forage Science*, *70*(4), 631–638.

Jones, H. P., Jones, P. C., Barbier, E. B., Blackburn, R. C., Rey Benayas, J. M., Holl, K. D., McCrackin, M., Meli, P., Montoya, D., & Mateos, D. M. (2018). Restoration and repair of Earth's damaged ecosystems. *Proceedings. Biological Sciences*, *285*(1873), 20172577. https://doi.org/10.1098/rspb.2017.2577

Kiehl, K., Kirmer, A., Donath, T. W., Rasran, L., & Hölzel, N. (2010). Species introduction in restoration projects — Evaluation of different techniques for the establishment of semi-natural grasslands in central and northwestern Europe. *Basic and Applied Ecology*, *11*(4), 285–299. https://doi.org/10.1016/j.baae.2009.12.004

Kirmer, A., Baasch, A., & Tischew, S. (2012). Sowing of low and high diversity seed mixtures in ecological restoration of surface mined-land. *Applied Vegetation Science*, *15*(2), 198–207. https://doi.org/10.1111/j.1654-109X.2011.01156.x

Köhler, M., Schmidt, A., Hölzel, N., Baasch, A., & Tischew, S. (2023). Positive long-term effects of year-round horse grazing in orchid-rich dry calcareous grasslands – results of a 12-year study. *Frontiers in Ecology and Evolution*, *11*, 1107987.

Laschke, C. J.*, Twerski, A.*, Bauer, M., Härdtle, W., Kirmer, A., Kollmann, J., Loos, J., Schmidt, A., Sturm, L., Tischew, S., Wiesmeier, M., & Temperton, V. M. (2026). Data and code for Laschke, Twerski et al. (2026) (v1.1.0) [Data set]. - Zenodo. https://doi.org/10.5281/zenodo.18621272

Laughlin, D. C., Chalmandrier, L., Joshi, C., Renton, M., Dwyer, J. M., & Funk, J. L. (2018). Generating species assemblages for restoration and experimentation: A new method that can simultaneously converge on average trait values and maximize functional diversity. *Methods in Ecology and Evolution*, *9*(7), 1764–1771.

Lenth, R. V. (2024). *emmeans: Estimated marginal means, aka least-squares means. Manual*. https://CRAN.R-project.org/package=emmeans

Leuschner, C., & Ellenberg, H. (2017). *Ecology of central European non-Forest vegetation: Coastal to Alpine, natural to man-made habitats: Vegetation ecology of Central Europe* (Vol. *II*). Springer.

LfU Bayern. (2022). *Kartieranleitung Biotopkartierung Bayern (inkl. Kartierung der Offenland-Lebensraumtypen der Fauna-Flora-Habitat-Richtlinie)—Teil 2—Biotoptypen*.

LfU SH. (2023). *Kartieranleitung und erläuterte Standardliste der Biotoptypen Schleswig-Holsteins—Version 2.2, Stand 04/23*, *228*.

Li, D. (2018). hillR: Taxonomic, functional, and phylogenetic diversity and similarity through Hill numbers. *The Journal of Open Source Software*, *3*(31), 1041. doi:10.21105/joss.01041

Lindborg, R., Hartel, T., Helm, A., Prangel, E., Reitalu, T., & Ripoll-Bosch, R. (2023). Ecosystem services provided by semi-natural and intensified grasslands: Synergies, trade-offs and linkages to plant traits and functional richness. *Applied Vegetation Science*, *26*(2), e12729. https://doi.org/10.1111/avsc.12729

Lyons, K. G., Török, P., Hermann, J.-M., Kiehl, K., Kirmer, A., Kollmann, J., & Temperton, V. M. (2023). Challenges and opportunities for grassland restoration: A global perspective of best practices in the era of climate change. *Global Ecology and Conservation*, *46*, e02612. https://doi.org/10.1016/j.gecco.2023.e02612

Maron, M., Juffe-Bignoli, D., Krueger, L., Kiesecker, J., Kümpel, N. F., ten Kate, K., Milner-Gulland, E. J., Arlidge, W. N. S., Booth, H., Bull, J. W., Starkey, M., Ekstrom, J. M., Strassburg, B., Verburg, P. H., & Watson, J. E. M. (2021). Setting robust biodiversity goals. *Conservation Letters*, *14*(5), e12816. https://doi.org/10.1111/conl.12816

Mehtälä, J., & Vuorisalo, T. (2007). Conservation policy and the EU habitats directive: Favourable conservation status as a measure of conservation success. *European Environment*, *17*(6), 363–375. https://doi.org/10.1002/eet.458

MULE. (2020). *Biotoptypenrichtlinie des Landes Sachsen-Anhalt. RdErl. des MULE vom 15.2. 2020–24.2-2247.—veröffentlicht in: MBl. LSA Nr. 19/2020 vom 2.6.2020*.

Nerlekar, A. N., Sullivan, L. L., & Brudvig, L. A. (2024). Grassland restorations must better foster forbs to facilitate high biodiversity. *Restoration Ecology*, *32*(7), e14214. https://doi.org/10.1111/rec.14214

Nerlekar, A. N., & Veldman, J. W. (2020). High plant diversity and slow assembly of old-growth grasslands. *Proceedings of the National Academy of Sciences of the United States of America*, *117*(31), 18550–18556. https://doi.org/10.1073/pnas.1922266117

Newbold, T., Hudson, L. N., Hill, S. L. L., Contu, S., Lysenko, I., Senior, R. A., Börger, L., Bennett, D. J., Choimes, A., Collen, B., Day, J., De Palma, A., Díaz, S., Echeverria-Londoño, S., Edgar, M. J., Feldman, A., Garon, M., Harrison, M. L. K., Alhusseini, T., … Purvis, A. (2015). Global effects of land use on local terrestrial biodiversity. *Nature*, *520*(7545), 45–50. https://doi.org/10.1038/nature14324

NLWKN. (2011). Artenreiches Nass-und Feuchtgrünland (außer Pfeifengras-und Brenndoldenwiesen). In *Niedersächsische Strategie zum Arten- und Biotopschutz. Vollzugshinweise zum Schutz der FFH-Lebensraumtypen sowie weiterer Biotoptypen mit landesweiter Bedeutung in Niedersachsen—Biotoptypen mit Priorität für Erhaltungs-und Entwicklungsmaßnahmen* (p. 15). NLWKN.

Noreika, N., Pärtel, M., & Öckinger, E. (2020). Community completeness as a measure of restoration success: Multiple-study comparisons across ecosystems and ecological groups. *Biodiversity and Conservation*, *29*(13), 3807–3827. https://doi.org/10.1007/s10531-020-02050-1

Pfadenhauer, J., Poschlod, P., & Buchwald, R. (1986). *Überlegungen zu einem Konzept geobotanischer Dauerbeobachtungsflächen für Bayern. Teil i. Ber. ANL*. https://www.zobodat.at/pdf/Ber-Bayer-Akad-f-Natursch-u-Landschaftspfl_10_1986_0041-0060.pdf

Prach, K., Fajmon, K., Jongepierová, I., & Řehounková, K. (2015). Landscape context in colonization of restored dry grasslands by target species. *Applied Vegetation Science*, *18*(2), 181–189.

Prach, K., Fajmon, K., Řehounková, K., & Jongepierová, I. (2021). Hierarchy of environmental factors driving restoration of dry grasslands: A multi-site analysis. *Applied Vegetation Science*, *24*(2), e12576.

Pywell, R. F., Bullock, J. M., Roy, D. B., Warman, L. I., Walker, K. J., & Rothery, P. (2003). Plant traits as predictors of performance in ecological restoration. *Journal of Applied Ecology*, *40*(1), 65–77. https://doi.org/10.1046/j.1365-2664.2003.00762.x

R Core Team. (2024). *R: A language and environment for statistical computing. Manual*. R Foundation for Statistical Computing. https://www.R-project.org/

Rey Benayas, J. M., Newton, A. C., Diaz, A., & Bullock, J. M. (2009). Enhancement of biodiversity and ecosystem services by ecological restoration: A meta-analysis. *Science (New York, NY)*, *325*(5944), 1121–1124. https://doi.org/10.1126/science.1172460

Roswell, M., Dushoff, J., & Winfree, R. (2021). A conceptual guide to measuring species diversity. *Oikos*, *130*(3), 321–338.

Schils, R. L., Bufe, C., Rhymer, C. M., Francksen, R. M., Klaus, V. H., Abdalla, M., Milazzo, F., Lellei-Kovács, E., ten Berge, H., Bertora, C., Chodkiewicz, A., Dămătîrcă, C., Feigenwinter, I., Fernández-Rebollo, P., Ghiasi, S., Hejduk, S., Hiron, M., Janicka, M., Pellaton, R., … Price, J. P. N. (2022). Permanent grasslands in Europe: Land use change and intensification decrease their multifunctionality. *Agriculture, Ecosystems & Environment*, *330*, 107891. https://doi.org/10.1016/j.agee.2022.107891

Schmiede, R., Otte, A., & Donath, T. W. (2012). Enhancing plant biodiversity in species-poor grassland through plant material transfer–the impact of sward disturbance. *Applied Vegetation Science*, *15*(2), 290–298.

Schüle, M., Heinken, T., & Fartmann, T. (2023). Long-term effects of environmental alterations in protected grasslands—Land-use history determines changes in plant species composition. *Ecological Engineering*, *188*, 106878. https://doi.org/10.1016/j.ecoleng.2022.106878

Shackelford, N., Dudney, J., Stueber, M. M., Temperton, V. M., & Suding, K. L. (2024). Measuring at all scales: Sourcing data for more flexible restoration references. *Restoration Ecology*, *32*(8), e13541. https://doi.org/10.1111/rec.13541

Shackelford, N., Paterno, G. B., Winkler, D. E., Erickson, T. E., Leger, E. A., Svejcar, L. N., Breed, M. F., Faist, A. M., Harrison, P. A., Curran, M. F., Guo, Q., Kirmer, A., Law, D. J., Mganga, K. Z., Munson, S. M., Porensky, L. M., Quiroga, R. E., Török, P., Wainwright, C. E., … Suding, K. L. (2021). Drivers of seedling establishment success in dryland restoration efforts. *Nature Ecology & Evolution*, *5*(9), 1283–1290. https://doi.org/10.1038/s41559-021-01510-3

Slodowicz, D., Durbecq, A., Ladouceur, E., Eschen, R., Humbert, J.-Y., & Arlettaz, R. (2023). The relative effectiveness of different grassland restoration methods: A systematic literature search and meta-analysis. *Ecological Solutions and Evidence*, *4*(2), e12221. https://doi.org/10.1002/2688-8319.12221

Tälle, M., Deák, B., Poschlod, P., Valkó, O., Westerberg, L., & Milberg, P. (2018). Similar effects of different mowing frequencies on the conservation value of semi-natural grasslands in Europe. *Biodiversity and Conservation*, *27*(10), 2451–2475. https://doi.org/10.1007/s10531-018-1562-6

Temperton, V. M., Pătru-Dușe, I. A., Twerski, A., Laeseke, P., Neudert, R., Cebrián-Piqueras, M. A., Romero, M. P., Bauer, M., Beckmann, V., Fischer, J., Gray, K., Härdtle, W., Kollmann, J., Kuhn, L., Laschke, C. J., Loos, J., Lutz, L., May, F., Meyer, M., … Kirmer, A. (2025). Proposing a social-ecological framework for successful grassland restoration in Germany—An overview and insights from the Grassworks project. *Restoration Ecology*, *33*(7), e70109. https://doi.org/10.1111/rec.70109

Tobisch, C., Rojas-Botero, S., Uhler, J., Müller, J., Kollmann, J., Moning, C., Brändle, M., Gossner, M. M., Redlich, S., Zhang, J., Steffan-Dewenter, I., Benjamin, C., Englmeier, J., Fricke, U., Ganuza, C., Haensel, M., Riebl, R., Uphus, L., & Ewald, J. (2023). Plant species composition and local habitat conditions as primary determinants of terrestrial arthropod assemblages. *Oecologia*, *201*(3), 813–825. https://doi.org/10.1007/s00442-023-05345-6

Török, P., Deák, B., Vida, E., Valkó, O., Lengyel, S., & Tóthmérész, B. (2010). Restoring grassland biodiversity: Sowing low-diversity seed mixtures can lead to rapid favourable changes. *Biological Conservation*, *143*(3), 806–812. https://doi.org/10.1016/j.biocon.2009.12.024

Török, P., Vida, E., Deák, B., Lengyel, S., & Tóthmérész, B. (2011). Grassland restoration on former croplands in Europe: An assessment of applicability of techniques and costs. *Biodiversity and Conservation*, *20*(11), 2311–2332. https://doi.org/10.1007/s10531-011-9992-4

Twerski, A., Bauer, M., Laschke, C. J., Wiesmeier, M., Sturm, L., Schmidt, A., Kollmann, J., Temperton, V. M., Kirmer, A., & Tischew, S. (2026a). *Vascular plant species occurrence and cover estimates of restored grasslands and reference sites in Germany* [dataset]. PANGAEA. https://doi.org/10.1594/PANGAEA.993406

Twerski, A., Bauer, M., Laschke, C. J., Wiesmeier, M., Sturm, L., Schmidt, A., Kollmann, J., Temperton, V. M., Kirmer, A., & Tischew, S. (2026b). *General vegetation characteristics of restored grasslands and reference sites in Germany* [dataset]. PANGAEA. https://doi.org/10.1594/PANGAEA.993401

UN. (2019). *United Nations Decade on Ecosystem Restoration (2021–2030). United Nations General Assembly Resolution 2019 A/RES/73/284*.

Vander Mijnsbrugge, K., Bischoff, A., & Smith, B. (2010). A question of origin: Where and how to collect seed for ecological restoration. *Basic and Applied Ecology*, *11*(4), 300–311. https://doi.org/10.1016/j.baae.2009.09.002

Von Gillhaussen, P., Rascher, U., Jablonowski, N. D., Plückers, C., Beierkuhnlein, C., & Temperton, V. M. (2014). Priority effects of time of arrival of plant functional groups override sowing interval or density effects: A grassland experiment. *PLoS One*, *9*(1), e86906. https://doi.org/10.1371/journal.pone.0086906

Waldén, E., & Lindborg, R. (2016). Long term positive effect of grassland restoration on plant diversity - success or not? *PLoS One*, *11*(5), e0155836. https://doi.org/10.1371/journal.pone.0155836

Wallis De Vries, M. F., Parkinson, A. E., Dulphy, J. P., Sayer, M., & Diana, E. (2007). Effects of livestock breed and grazing intensity on biodiversity and production in grazing systems. 4. Effects on animal diversity.

Grass and Forage Science, *62*(2), 185–197. https://doi.org/10.1111/j.1365-2494.2007.00568.x
Weidlich, E. W. A., Nelson, C. R., Maron, J. L., Callaway, R. M., Delory, B. M., & Temperton, V. M. (2021). Priority effects and ecological restoration. *Restoration Ecology*, *29*(1), e13317. https://doi.org/10.1111/rec.13317
Werner, C. M., Stuble, K. L., Groves, A. M., & Young, T. P. (2020). Year effects: Interannual variation as a driver of community assembly dynamics. *Ecology*, *101*(9), e03104. https://doi.org/10.1002/ecy.3104
Wilson, J. B., Peet, R. K., Dengler, J., & Pärtel, M. (2012). Plant species richness: The world records. *Journal of Vegetation Science*, *23*(4), 796–802. https://doi.org/10.1111/j.1654-1103.2012.01400.x
Wirth, C., Bruelheide, H., Farwig, N., Marx, J. M., & Settele, J. (2024). *Faktencheck Artenvielfalt*. oekom Verlag.
Wortley, L., Hero, J.-M., & Howes, M. (2013). Evaluating ecological restoration success: A review of the literature. *Restoration Ecology*, *21*(5), 537–543. https://doi.org/10.1111/rec.12028
Zobel, M. (2016). The species pool concept as a framework for studying patterns of plant diversity. *Journal of Vegetation Science*, *27*(1), 8–18. https://doi.org/10.1111/jvs.12333
Zuur, A. F., & Ieno, E. N. (2016). A protocol for conducting and presenting results of regression-type analyses. *Methods in Ecology and Evolution*, *7*(6), 636–645. https://doi.org/10.1111/2041-210X.12577

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Effect of restoration on a suite of different diversity variables: (a) total plant species richness, (b) characteristic plant species richness (grasslands), (c) Hill–Shannon diversity for total and (d) characteristic effective number of species (ENS), (e) Favourable Conservation Status (FCS_i), and (f) forb-graminoid ratio compared with negative and positive reference sites in three regions (north, centre, south). All variables relate to 16 m^2; neg, negative reference sites; rest, restored sites; pos, positive reference sites.

Figure S2. Effect of different restoration methods in three regions (north, centre, south) on (a) total and (b) characteristic species richness, (c) Hill–Shannon diversity for total and (d) characteristic effective number of species (ENS), (e) Index of Favourable Conservation Status (FCS_i), and (f) forb-graminoid ratio. All variables relate to 16 m^2; cus, sowing of cultivar seed mixtures; mga, management adaptation; res, sowing of regional seed mixtures; dih, sowing of directly harvested material.

Figure S3. Effect of restoration in three soil moisture levels (moist, fresh, dry) on a suite of different diversity variables: (a) total plant species richness, (b) characteristic plant species richness (grasslands), (c) Hill–Shannon diversity for total and (d) characteristic effective number of species (ENS), (e) Favourable Conservation Status (FCS_i), and (f) forb-graminoid ratio compared with negative and positive reference sites. All variable relate to 16 m^2; neg, negative reference sites; rest, restored sites; pos, positive reference sites.

Figure S4. Effect of different restoration methods (cus, sowing of cultivar seed mixtures; mga, management adaptation; res, sowing of regional seed mixtures; dih, sowing of directly harvested material) in three soil moisture levels (moist, fresh, dry) on (a) total and (b) characteristic species richness, (c) Hill–Shannon diversity for total and (d) characteristic effective number of species (ENS), (e) Index of Favourable Conservation Status (FCS_i), and (f) forb–graminoid ratio. All variables relate to 16 m^2.

Figure S5. Effect of restoration on forb, legume, and graminoid cover. Neg, negative reference sites; pos, positive reference sites; rest, restored sites. All variables relate to 16 m^2.

Figure S6. Effect of different restoration methods (cus, sowing of cultivar seed mixture; mga, management adaptation; res, sowing of regional seed mixtures; dih, sowing of directly harvested material) on forb, legume, and graminoid cover. Neg, negative reference sites; pos, positive reference sites; and rest, restored sites; all variables relate to 16 m^2.

Table S1. Adapted Brown–Blanquet scale used in *Grassworks* for vegetation surveys following (Pfadenhauer et al., 1986) but using adapted cover and mean coverage per species. This allowed for total cover percentages of over 100% for plant communities.

Table S2. Results of the generalised linear mixed models (sites younger 20 years) with different restoration factors (restoration method, previous land use) for different response variables (total and characteristic species richness, total and characteristic Hill–Shannon diversity, forb-graminoid ratio, and Index of Favourable Conservation Status (FCS_i)). Levels of significance: $^{*}p<0.05$, $^{**}p<0.01$, $^{***}p<0.001$. Region and hydrology are used as random factors in the models. Est, estimate; SE, standard error; *z*, *z*-value.

Table S3. Estimated marginal means (EMM) and standard error (SE) of restored and reference sites (positive, negative) in generalised linear mixed models with different response variables (total and characteristic species richness per 16 m^2, total and characteristic Hill–Shannon diversity per 16 m^2, Index of Favourable Conservation Status (FCS_i) and forb-graminoid ratio). Letters (sign.) indicate significant differences ($p<0.05$) based on Tukey-adjusted pairwise comparisons of EMMs.

Table S4. Estimated marginal means (EMM) and standard error (SE) of restoration methods in generalised linear mixed models with different response variables (total and characteristic species richness per 16 m^2, total and characteristic Hill–Shannon per 16 m^2, Index of Favourable Conservation Status (FCS_i) and forb-graminoid ratio). Letters (sign.) indicate significant differences ($p<0.05$) based on Tukey-adjusted pairwise comparisons of EMMs.

Table S5. Taxonomic entities ($n=572$) of all vascular plants found in 187 study sites. The table shows characteristic grassland plant species (n = 335) according to three lists of characteristic species (EUNIS-Esy, Habitat Directive, Calthion) in bold.

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