Received: 9 March 2023 | Accepted: 8 August 2023

DOI: 10.1111/1365-2664.14497

Journal of Applied Ecology BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Fit by design: Developing seed–substrate combinations to adapt dike grasslands to microclimatic variation

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Funding information
Deutsche Bundesstiftung Umwelt, Grant/Award Number: 20021/698; WIGES GmbH, Grant/Award Number: 80002312

Handling Editor: Lan Qie

Abstract

1. Sowing is a well-established restoration technique to overcome dispersal limitation. Seed mixtures adapted to certain environmental conditions, like substrate or microclimate, are most effective to achieve functional communities. This is especially important if the restored vegetation has to protect critical infrastructure like roadsides and dikes. Here, an improved seed–substrate combination will secure slope stability, make restorations more effective and generate species-rich grasslands.
2. A full-factorial field experiment addressed this topic on a dike at River Danube in SE Germany in 2018–2021. Within 288 plots, we tested three sand admixtures, two substrate depths, two seed densities and two seed mixture types (mesic hay meadow and semidry calcareous grassland) in north and south exposition and measured the recovery completeness by calculating the successional distance to reference sites, the persistence of sown species and the Favourable Conservation Status (FCS) of target species.
3. Overall, the sown vegetation developed in the desired direction, but a recovery debt remained after 4 years, and some plots still showed similarities to negative references from ruderal sites. In north exposition, hay meadow seed mixtures developed closer to their reference communities than dry grassland mixtures to their reference.
4. In south exposition, the sown communities established poorly, which might be due to a severe drought during establishment. This initial negative effect remained over the entire observation period.
5. Sand admixture had a slightly positive effect on target variables, while the tested substrate depths, seed densities and seed mixture types had no effects on species persistence or FCS.
6. *Synthesis and applications*: Site-adapted seed mixtures make restoration more effective, while applying several seed–substrate combinations might foster beta diversity. Furthermore, additional management efforts are recommended, as they might be necessary to reduce the recovery debt, as well as re-sowing after unfavourable conditions like droughts.

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KEYWORDS
artificial soil mixture, dry grasslands, ecological restoration, levee, persistence, river embankment, sowing, species composition

1 | INTRODUCTION

Grasslands can support an exceedingly high biodiversity, and they provide several ecosystem services (Bengtsson et al., 2019; Dengler et al., 2014). However, they are globally endangered (Bardgett et al., 2021), and in Europe, calcareous grasslands and hay meadows are red-listed habitats (Category 3, 'vulnerable', Janssen et al., 2016). Restoration is seen as a key factor to sustain biodiversity and ecosystem services (Convention on Biological Diversity (CBD), 2014; United Nations, 2019), and sowing is a well-established approach to establish species-rich grasslands (Kiehl et al., 2010). Sowing high-diversity mixtures of regional provenance (Bucharova et al., 2019) produced by specialised companies is a promising way to scale up restoration efforts (Freitag et al., 2021) and to overcome dispersal filters (Myers & Harms, 2009; Orrock et al., 2023). However, there are still open questions about adjusting seed mixtures to specific site conditions and future climate conditions (Török et al., 2021).

Restoration ecology can increase the predictability of restoration approaches (Mouquet et al., 2015) by using rigorous, repeatable and transparent experiments based on advanced theory, which will finally strengthen evidence-based restoration (Cooke et al., 2018; Wainwright et al., 2018). Local site conditions and the restoration method are key predictors for vegetation development after sowing (Brudvig et al., 2017). The main assembly processes are habitat and biotic filtering, which can be manipulated by the choice of seed–substrate combinations (Török & Helm, 2017). This means a close adaptation of the substrate to the niche of the target species or of the seed mixtures to the characteristics of the chosen substrate. Suitable substrates reduce habitat filtering of the seeded species, while specific seed mixtures minimise competitive exclusion of desired species and simultaneously prohibit invasive species by niche saturation (Funk et al., 2008). Modifying seed mixtures to match the site conditions could be based on functional plant traits (Balazs et al., 2020; Funk et al., 2008; Laughlin, 2014), although this is not easy to implement (Bauer et al., 2022; Merchant et al., 2022). This challenge is particularly interesting for artificial substrates that can be modified and are often used in urban areas (Bauer et al., 2022), quarries (Chenot-Lescure et al., 2022) or river dikes (Liebrand & Sykora, 1996).

River dikes are promising sites for the restoration of species-rich grasslands because they can increase habitat area and connectivity of semi-natural grasslands and therefore significantly contribute to biodiversity conservation in agricultural landscapes (Bátori et al., 2020). Several ecosystem functions can be reconciled by dike grasslands like erosion control and biodiversity (Berendse et al., 2015; Husicka, 2003; Teixeira et al., 2022), which can be fostered by an adapted seed–substrate combination. Experiments with such seed–substrate combinations on dikes benefit from contrasting microclimates of the different expositions of the steep slopes (>1:3) (Suggitt et al., 2011).

The aim of this study was to identify the best combinations of seed mixtures and substrates for vital and species-rich grasslands on north- and south-exposed dike slopes. Thus, an experiment was set up to test different substrate depths, sand admixtures, seed densities and seed mixture types. We expected to see a better development of dry grasslands in the south exposition, with a shallow and sandy substrate, and of hay meadows in north exposition on a less sandy and deeper substrate. In general, we expect a better development on sandy and shallow substrate because nutrient availability is reduced (Baer et al., 2004). On steep slopes, such as dikes, high seed densities are recommended for successful establishment of vegetation (Kleber-Lerchbaumer et al., 2017), albeit without experimental evidence.

The success of restoration, that is, the difference from desired conditions, is evaluated by comparing the species composition with reference sites (cf. Brudvig et al., 2017), since the successional distance to reference grasslands describes the recovery completeness (Rydgren et al., 2019). Furthermore, we observed the persistence, which is the presence of the sown species monitored over three consecutive years (Wilsey, 2021). Finally, the Favourable Conservation Status (FCS) was calculated, which distinguishes habitat-characteristic diversity and non-typical derived diversity (Helm et al., 2015). Based on 4 years of monitoring, we tested the following hypotheses:

1. Site conditions on northern vs southern dike slopes facilitate establishment of hay meadow or dry grassland mixtures, respectively.
2. Nutrient reduction by sand admixture and shallow substrates improve the establishment of dry grassland seed mixtures compared with hay meadow mixtures.
3. High seed densities and reduced soil fertility improve the establishment of sown plants and suppress non-target species compared with low density sowing and high soil fertility.

2 | MATERIALS AND METHODS

2.1 | Field experimental design

Specific combinations of seed mixtures and substrates ('seed–substrate combinations') were tested on an existing dike covered by grassland at the Danube River in SE Germany (Figure 1; 314 m a.s.l.; WGS84: lat/lon, 48.83895/12.88412). The climate of the region is temperate-suboceanic with a mean annual temperature of 8.4°C and

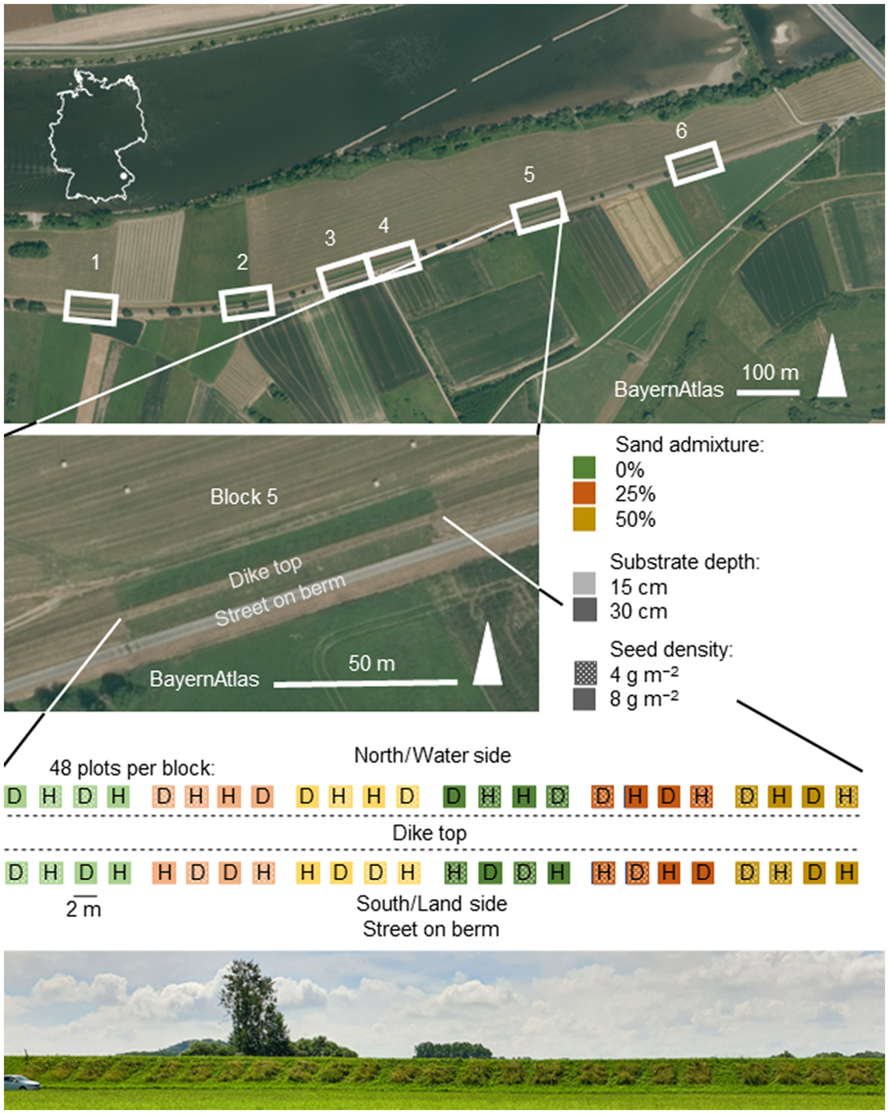

FIGURE 1 Local setting and design of the multifactorial experiment on grassland sowing on dikes. The experiment was located on a dike at River Danube in SE Germany. The 288 plots were allocated in six blocks (white squares on the upper photograph) and on the north and south slope (central photograph; both aerial photographs: Bayerische Vermessungsverwaltung, 2023). Four treatments were conducted: sand admixture, substrate depth, seed density and seed mixture types H and D (hay meadows and dry grasslands). The western half of a block had a shallow substrate depth, and within this, half of the substrates had different sand admixtures. The photograph on the bottom shows the northern slope of one block in 2021, 4 years after sowing (photograph: Markus Bauer).

an annual precipitation of 984 mm (Deutscher Wetterdienst, 2021). During the study, three exceptionally dry years (2018–2020) occurred (Appendix S1, Hari et al., 2020), as well as three minor floods, which, though, did not reach the plots (Appendix S1). The substrates consisted of calcareous sand (0–4 mm grain size) and agricultural soil obtained from a nearby dike construction site near the village of Steinkirchen. A big roller mixed both components and an excavator filled the substrates into the dug plots.

The target vegetation types were typical grassland types for Central Europe: lowland mesic hay meadows and semi-dry calcareous grassland (EUNIS codes: R22, R1A, Chytrý et al., 2020; Arrhenatherion elatioris and Cirsio-Brachypodion pinnati according to the EuroVegChecklist: CM01A, DA01B, Mucina et al., 2016). The species pool for seed mixtures of hay meadows and dry grasslands consisted of 55 and 58 species, respectively. The seeds were supplied by a commercial producer of autochthonous seeds (Co. Krimmer, Pulling, source area 16, Prasse et al., 2010). From these species pools, 20 species were selected for each plot in a stratified randomised manner (Appendix S2). The aim of these random and unique subsamples was to test types of seed mixtures and not only two certain species compositions. Each mixture contained seven grasses (60 wt% of total seed mixture), three legumes (5%) and 10 further non-legume forbs (35%; Table 1). The hay meadow mixtures had higher community-weighted means for specific leaf area, lower means for seed mass and higher ones for canopy height than the dry grassland mixtures (Appendix S3). The south-exposed plots were sown in mid-April 2018 and the north exposed 14 days later. In late April 2018 due to the drought, the south exposition was protected by a geotextile consisting of straw chaff (350 g m^{-2}), which was removed after 2 weeks due to unsatisfactory effects on seedling emergence. In October 2018, *Bromus hordeaceus* was sown as a nursery grass to provide safe sites under drought conditions. The management started with a cut at 20 cm height without hay removal in August 2018, followed by standard deep cuts with hay removal in July 2019 and 2020. The surrounding area of the plots was mown thrice a year and the first time before flowering in May.

We used 288 plots of the size 2.0 × 3.0 m, vertically oriented, halfway up the dike slopes (1:2), distributed over the north and south exposition and arranged in six blocks (=replicates). The experiment used a split-plot design combined with a randomised complete block design (Figure 1). The split plot was created by the two expositions of the dike, where all 24 treatment combinations were tested, that is, sand admixtures (0%, 25% and 50%), soil depths (15 vs. 30 cm), two seed mixture types and two seed densities (4 vs. 8 g m^{-2}). Kiehl et al. (2010) recommend 1–5 g m^{-2} for grassland restoration, and Kleber-Lerchbaumer et al. (2017) recommend an increased density of 5–8 g m^{-2} for slopes.

Below the substrate, a 5-cm-thick drainage layer of gravel (0–16 mm grain size) was installed. Soil samples of the three substrates from both expositions were tested by mixing several subsamples from different plots. The sand admixture changed the soil texture, increased the C/N ratio and reduced calcium carbonate, but did hardly change the pH which was within the weak alkaline range (Table 2). Husicka (2003) recommends soil properties for dike substrates: the pH values and C/N ratios of the tested substrates were within the recommended ranges. Furthermore, the clay ratio was within the proposed range for the treatment 25% sand admixture and the substrate depth for the treatment of 30 cm depth (Husicka, 2003). Phosphate and potassium were rather scarce for agricultural soils, but magnesium showed high concentrations (Bayerisches Landesamt für Landwirtschaft (LfL), 2022).

TABLE 1 Each plot received an individual set of 20 species with some restrictions to the number of species per functional group. The total species pool for the seed mixture for hay meadows was 55 and for dry grassland 58 (in total 93 different species). All individual seed mixtures are stored in Appendix S2.

Functional group	Species pool		Seed mixture	Total ratio	Ratio per species
	Hay meadow	Dry grassland			
	#	#	#	wt%	wt%
High grasses	6	5	3	25.7	8.6
Low grasses	8	8	4	34.3	8.6
Legumes	5	7	3	5.0	1.7
Forbs	34	36	9	30.0	3.3
Hemiparasites	2	2	1	5.0	5.0

2.2 | Vegetation surveys

The vegetation was surveyed in June or July 2018–2021 (Braun-Blanquet, 1964), and the Londo scale was used (Londo, 1976). No special permits were necessary. The establishment rates of species were recorded in Appendix S4. Establishment success was high with 48 species of the species pool of hay meadows (87%) and 46 (79%) of dry grasslands recorded by 2021, which are rather good ratios (cf. Hedberg & Kotowski, 2010); the species established in 31 ± 22% (mean ± SD) of their sown plots. In total, 274 vascular plant species were found (Appendix S5).

To compare the restoration outcomes with real references and not solely with seed mixtures, vegetation surveys were extracted from sPlotOpen (Sabatini et al., 2021) and our own surveys on the Danube dikes in the surroundings (Bauer et al., 2023a). We selected six dry grassland plots (EUNIS code R1A, Chytrý et al., 2020) within SE Germany from sPlotOpen and 82 plots of our own survey, which included dry grasslands ($n = 15$), hay meadows (R22, $n = 59$), and as a negative reference ruderal, dry and anthropogenic vegetation (V38, $n = 9 \times 2$, plots used for both seed mixture types).

The recovery completeness was described by the successional distance, which quantifies the distance of a plot to the average reference site in the ordination ($d_{jt,0}$, Rydgren et al., 2019, Figure 2). Persistence was derived from the 'species losses' component of the temporal beta-diversity index (TBI; $1 - B_{sor}$), which was calculated by comparing the seed mixtures with the respective species composition of each year using Sørensen dissimilarity (Legendre, 2019). The

TABLE 2 Characteristics of the substrates used for the sowing experiment on river dikes. Soil samples of the three substrates were taken from 0 to 25 cm with a hand drill of 3.3 cm diameter and were analysed for the fraction <2 mm. The soil texture was classified according to the 'Bodenkundliche Kartieranleitung' (Bundesanstalt für Geowissenschaften und Rohstoffe, 2005), and the pH was measured in $CaCl_2$ solution. Plant-available phosphorus and potassium were measured in a calcium acetate-lactate extract and magnesium in a $CaCl_2$ extract. For calculating $CaCO_3$, a subsample was annealed at 550°C and the measured C amount multiplied with 8.33. To calculate total N and the C/N ratio, a subsample was incinerated at 1000°C. Lt3 = medium clayey loam; Ls4 = strong sandy loam; Sl3 = medium loamy sand; Sl4 = strong loamy sand

Exposition	Sand admixture	Skeleton (>2 mm)	Sand	Silt	Clay	Soil texture	pH	N	P_2O_5	K_2O	Mg^{2+}	C/N	$CaCO_3$
	vol%	vol%	wt%	wt%	wt%			wt%	mg 100 g^{-1}	mg 100 g^{-1}	mg 100 g^{-1}		wt%
North	0	5	18	45	37	Lt3	7.4	0.35	4	6	27	8.9	12.1
	25	26	49	29	22	Ls4	7.4	0.24	4	5	25	9.0	8.8
	50	40	75	14	11	Sl3	7.5	0.11	3	4	17	9.5	5.3
South	0	9	18	45	37	Lt3	7.3	0.37	6	7	28	8.8	12.5
	25	26	59	23	18	Ls4	7.4	0.19	3	5	23	9.2	7.3
	50	44	71	18	13	Sl4	7.5	0.13	4	5	16	9.5	7.3

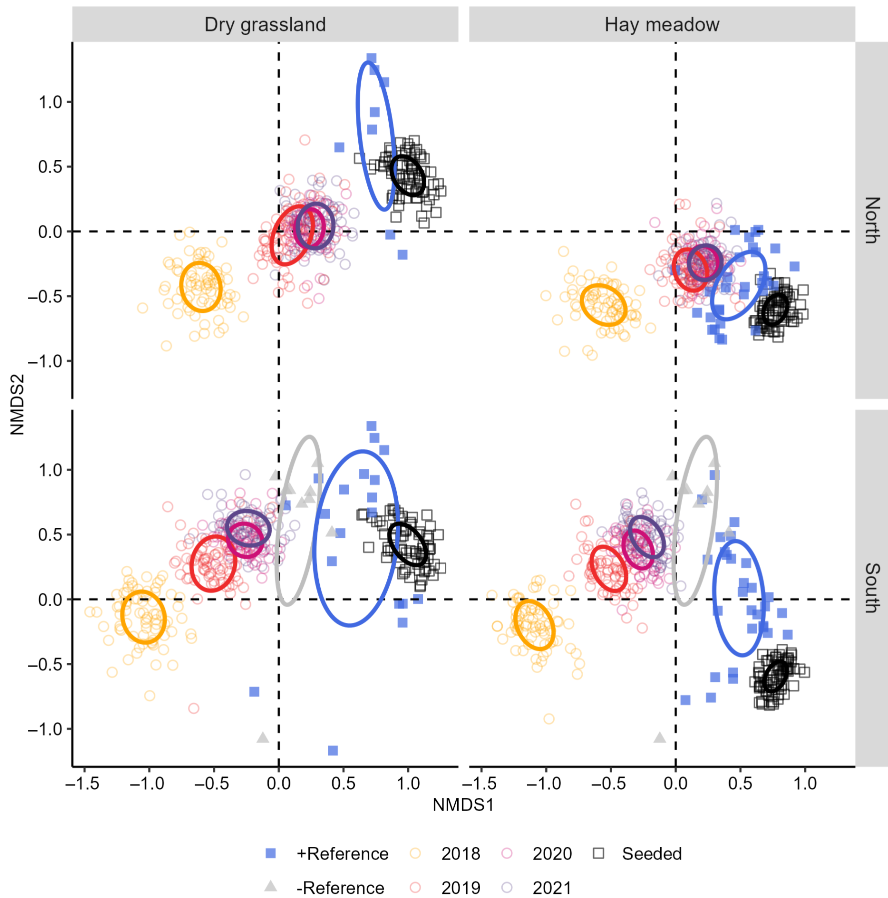

FIGURE 2 Species composition of sown experimental plots on a river dike over time and in comparison with reference sites and the seed mixtures. Both expositions and both seed mixture types are shown in separate panels. The non-metric multidimensional scaling ordination (NMDS) was based on the Sørensen dissimilarity and data of 288 plots (72 per panel) observed over 4 years after sowing in 2018 (circles). These experimental plots were compared with the seed mixtures (black squares, 72 per panel) and 89 positive and negative reference plots (filled symbols, 8–38 per panel) from older dike grasslands in the surroundings (Bauer et al., 2023a) and from sPlotOpen (Sabatini et al., 2021). The ellipses show the standard error of the groups. 2D-stress: 0.21.

FCS is the ratio of characteristic and derived diversity measured as species richness (Helm et al., 2015). Characteristic diversity consists of species that belong to a habitat-specific species pool and derived diversity consists of all other species. The habitat-specific species pool consisted of all sown species and other typical species of hay meadows and dry grasslands (Appendix S5).

2.3 | Statistical analysis

A nonmetric multidimensional scaling ordination (NMDS) with Sørensen dissimilarity (presence–absence data) was used to visualise variation in species composition in space and time. Seven species were excluded because they had an accumulated cover over all plots of <0.5%. Finally, 343 species were included in the ordination.

To measure the effects of the treatments on our three response variables, we calculated Bayesian linear mixed-effects models with the random effect plot nested in block with the Cauchy prior (see Lemoine, 2019). Furthermore, we included as a fixed effect the botanists, who recorded a certain plot. For the simple effects of the treatments (sand admixture, substrate depth, seed density, seed mix and exposition), we chose plausible weakly informative priors. To evaluate the influence of the priors, prior predictive checks and models with non-informative priors were calculated.

For the computation, we used four chains, a thinning rate of two, 5000 iterations for warm-up and 10,000 in total. We used the Markov Chain Monte Carlo method (MCMC) with the No-U-Turn Sampler. For evaluating the computation, the convergence of the four chains was checked using trace plots and evaluating *R*-hat values and MCMC chain resolution by the effective sampling size. Posterior predictive checks were done with Kernel density estimates histograms of statistics skew and leave-one-out cross-validation (see Gabry et al., 2019). Finally, the models were compared with the Bayes factor and Bayesian R^2 values (Gelman et al., 2019).

Data, code and the entire model specifications and evaluations are stored on Zenodo and presented on GitHub in an easily accessible document for scrolling through (Bauer et al., 2023b). There, the sections are referenced to the Bayesian analysis reporting guidelines (BARG, Kruschke, 2021). All analyses were performed in R (Version 4.2.3, R Core Team, 2022), with the functions 'brm' from the package 'brms' (Bürkner, 2017) for model calculation, several functions from 'brms' and 'bayesplot' for model evaluation (Gabry & Mahr, 2022), and 'metaMDS' from 'vegan' for the ordination (Oksanen et al., 2022).

3 | RESULTS

3.1 | Hay meadows on north exposition closer to reference

The ordination showed the species composition of seed mixtures and the development of the plots during 4 years (Figure 2;

2D-stress: 0.21). The NMDS confirmed that the seed mixtures were variable, albeit distinctive for hay meadows and dry grasslands, and confirming the intended direction of the vegetation development. As one exception, hay meadows in south exposition did not develop towards their seed mixture compositions as expected in hypothesis 1 (H1).

The reference sites had a larger variation than the seed mixtures and were close to the seed mixtures but hardly overlapped (Figure 2). The positions of the reference sites shifted to the left in comparison with the seed mixtures, which means in the direction of early-successional stages. Nonetheless, they still differed from the negative references of ruderal vegetation. Negative references were only available on southern slopes, and they were located in the NMDS between the positive reference sites and the state of restored plots in 2021. Nevertheless, 33% of the 288 plots reached the state of the target habitat types by 2021 (EUNIS code R22, R1A, Chytrý et al., 2020). Hay meadow seed mixtures led to a closer development to hay meadow references than dry grasslands to their references (Figures 3a and 4a). This was especially the case in north exposition (H1; Figure 2).

3.2 | Weak effects of substrates and seed density

A statistically clear positive effect of the sand admixture (H2) was identified on the persistence of sown species and on the recovery rate, but no effects by substrate depth (H2) or seed density (H3; Figure 3; Persistence: $R^2_m=0.86$, $R^2_c=0.89$; Recovery: $R^2_m=0.90$, $R^2_c=0.92$; FCS: $R^2_m=0.81$, $R^2_c=0.85$). The posterior distributions are also shown in the interaction plots that separate exposition and survey year (Figure 4). For all three response variables, the vegetation developed positively after 1 year, while the recovery rate slowed down in the following years. Both expositions revealed similar trends but for all responses, the values were clearly lower in south exposition; for example, persistence values were on average more than 46% higher in north exposition (Figure 4b). The interactions of restoration treatments were neither clear nor strong (H2, H3). Persistence of both seed mixture types was slightly positively affected by sand admixture in north exposition (H2; +6–7±4%, Figure 4b).

4 | DISCUSSION

4.1 | Success of the restoration approaches

The seed mixtures and their positive reference sites were similar but hardly overlapped (Figure 2). The position on the ordination suggests that the seed mixture represents a late-successional stage compared with the positive references. The NMDS shows a slightly better adaptation of the hay meadows to the north exposition than the dry grasslands. This effect, albeit stronger, was expected in H1 (Figure 4a). This can be expected from the requirements of hay meadows for mesic conditions, which can be provided on north-exposed dike slopes (Bátori et al., 2020; Oberdorfer, 1993). In south exposition, the hay meadow plots developed rather towards dry grassland references, which indicates an ineffective restoration due to seed mixture which is not adapted to the microclimatic conditions of southern slopes.

The vegetation developed generally in the desired direction. The development after 1 year was very fast and afterwards very slow. For practitioners, it would be more cost-efficient to start monitoring not in the year of seeding because ruderal species are too dominant for a sensible interpretation of the results. After 4 years, the vegetation was still distinct from positive references and seed mixtures. In the south exposition, the plots were rather similar to the negative reference of dry ruderal vegetation typical of grassland restoration when perennial species are still developing to become dominant (Eckhoff et al., 2023). The gap between goal and restoration outcome was also shown for other sowing experiments or restorations (Engst et al., 2016; Kaulfuß et al., 2022; Mitchley et al., 2012) or for dike vegetation compared with semi-natural reference grassland (Bátori et al., 2016). This result is not surprising since the 'recovery debt' is a general phenomenon of grassland restoration (Jones et al., 2018; Moreno-Mateos et al., 2017), and 5 years might be too short for the assembly of secondary grasslands (cf. Nerlekar & Veldman, 2020). The annual *B. hordeaceus*, seeded in autumn 2018 as nursery plant, decreased but was still present in 179 of 288 plots in 2021. Reasons for the recovery debt might not only be abiotic conditions but can also be biotic factors like missing mycorrhiza in the substrates (Koziol & Bever, 2017), or the post-restoration management needs to be developed (Tölgyesi et al., 2022).

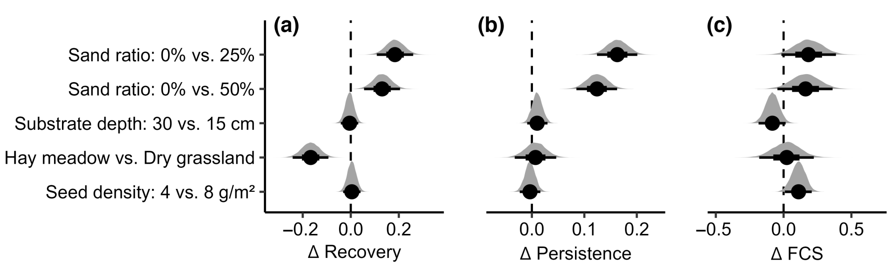

FIGURE 3 Effects of treatments on the development of sown grassland communities at a river dike. The posterior density distributions (grey) are calculated over all four surveyed years and both expositions. Shown are the medians, 66% and 95% credible intervals, which were derived from a Bayesian linear mixed-effects model. Shown are (a) the recovery completeness compared with reference sites, (b) the persistence of sown species and (c) the Favourable Conservation Status (FCS). The FCS is the ratio of target species to non-target species. Note that the zero lines indicate that both levels have equal values. This means, for example, that hay meadows are closer to their reference than dry grasslands or 25% sand admixture was closer to its reference than 0% addition (a).

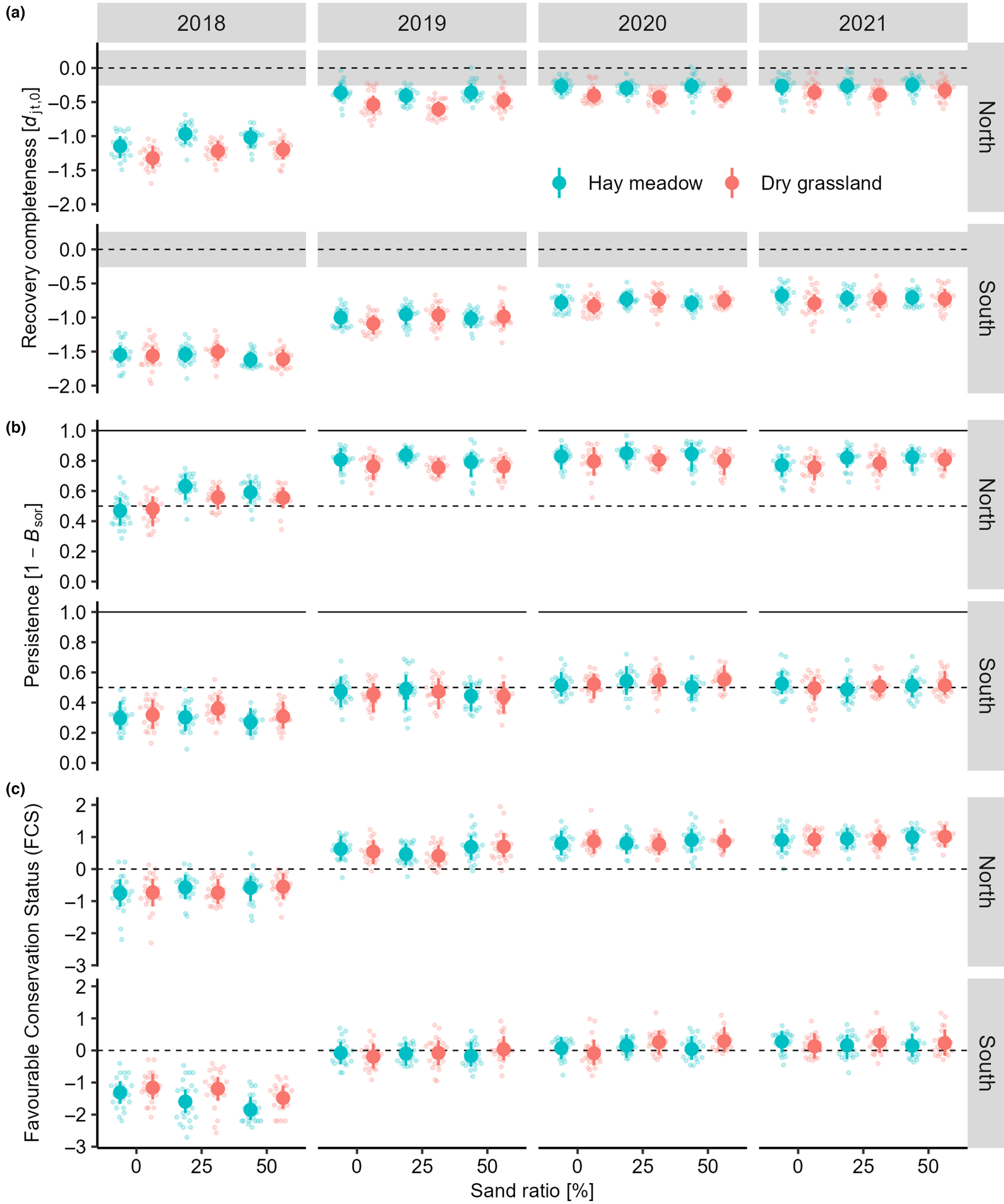

FIGURE 4 Development of grassland communities at a river dike over 4 years after sowing. The plots had substrates with different sand admixtures and were sown with two different seed mixture types. Three indices are evaluated. (a) Recovery completeness ($d_{jt,0}$): the zero lines indicate the mean position of the reference sites for each habitat type on the NMDS axis 1 (Figure 2). The grey area marks the standard deviation of the position of the reference sites (Figure 2). (b) Persistence of sown species: losses component of the temporal beta-diversity index ($1 - B_{sor}$). (c) Favourable Conservation Status (FCS): the zero line indicates that target and non-target species are balanced. Positive values indicate that there are more target species. Shown are the medians and 95% credible intervals of the posterior distributions, which were derived from a Bayesian linear mixed-effects model.

4.2 | General effects of treatments and exposition

Restoration on agricultural soils can have limited success due to high nutrient loads (Walker et al., 2004), and mixing with a mineral component does not necessarily improve the outcome (Chenot-Lescure et al., 2022). Similar to Chenot-Lescure et al. (2022), sand admixture reduced nutrient loads and led to higher persistence of sown species as expected by H2, while an increase from 25% to 50% admixture did not further increase this effect. In addition, the effect only appeared in north exposition and the effect size of about 6% in the 4th year of restoration was rather small. The FCS was hardly affected by the sand admixture, which corresponds to an experiment in a quarry (Chenot-Lescure et al., 2022) but not to our expectations (H2). An increase in substrate depth from 15 to 30 cm did neither significantly affect persistence nor FCS, similar to earlier studies (Baer et al., 2004; Husicka, 2003). Larger differences in soil depths might be necessary to observe negative effects by thicker substrate layers as was shown for prairies (Dornbush & Wilsey, 2010) or a thin substrate layer of <15 cm, since most roots occur in the topsoil on dikes (Vannoppen et al., 2016). Seed density had also no clear effect on persistence and FCS, which is contrary to H3 but fits the results of Kaulfuß et al. (2022), who found that a certain amount of seeds is necessary for a successful establishment of target species, but higher densities do not further improve the outcome, and rather have a slightly negative effect.

The vegetation in south exposition had a more ruderal and xerophytic species compositions than in north exposition, which contrasts Bátori et al. (2016) who found different compositions in south exposition only for riverside slopes that caused a more mesotrophic vegetation. The differences in our experiment might be due to methodical reasons, since the geotextile, which had been implemented on the southern slope, was removed after 2 weeks. This was unfortunate for at least some seedlings and amplified by the intense drought in summer 2018 and 2019 (cf. Hari et al., 2020; Larson et al., 2021; Orrock et al., 2023). The lasting negative effect on persistence and FCS on the southern slope suggests a legacy effect of adverse weather conditions after sowing as observed by other studies (Atkinson et al., 2023; Groves et al., 2020). These conditions during the establishment phase might have led to a special trajectory (Suding et al., 2004) and probably levelled the distinction of the seed mixture types in south exposition.

4.3 | No interaction effect of seed–substrate combinations

Our aim was to identify perfect seed–substrate combinations regarding restoration effectiveness and biodiversity (H2, H3). For evaluating effectiveness, we measured the persistence of the sown species, and FCS for investigating plant biodiversity. However, we could not identify an interaction effect for any of these indices. We would have expected a better performance of hay meadow seed mixtures with lower sand admixture and for dry grasslands with higher sand admixture (H2). Our results suggest that, at least after 4 years, the substrate conditions are within the range of both seed mixture types (hay meadows vs. dry grasslands). Although both types are clearly phytosociologically and functionally distinct, they are still relatively close, because they contain shared species and develop under similar site conditions with modified subassociations (Appendix S3, Husicka, 2003; Oberdorfer, 1993). Other grassland studies could identify more or less clear interactions of opposing habitat preferences or functional traits along the gradients of productivity, moisture and nutrients (Freitag et al., 2021; Kaulfuß et al., 2022; Zirbel & Brudvig, 2020). However, these studies did not work with an experimental set-up of different seed–substrate combinations, but analysed the result of habitat and biotic filtering after 1, 5 and 15 years, respectively. Furthermore, the non-existence of ideal combinations could be explained by priority effects, which means that the species of the imperfect-adapted seed mixture type could establish earlier and pre-empted the available niches for the species of related habitat types (Fukami, 2015).

5 | CONCLUSIONS

Our results suggest that adapted seed mixtures can increase restoration effectiveness by sowing hay meadows in the north but not necessarily in south exposition of dikes. Furthermore, the reduction of the nutrient load through sand admixture was positive, albeit with small effect size. The question remains if sand admixture is the most efficient restoration measure to promote diversity on dikes. Increasing seed density on dike slopes does not appear to be necessary which contradicts common recommendations (Kleber-Lerchbaumer et al., 2017), and soil depths of 30 cm are not adverse compared with 15-cm-thick substrates.

There were no perfect seed–substrate combinations, and thus, we conclude that a variation of seed mixture types and different substrates along restoration sections would promote biodiversity more than a single solution (Bauer et al., 2023a; Holl et al., 2022). Negative effects of drought in the sowing season might require re-seeding. Restoration projects should account for the increasing frequency of droughts (Naumann et al., 2018) by re-seeding or by combining seeding with hay transfer (Török et al., 2012) to improve the microclimate during establishment (Eckstein & Donath, 2005). We expect a minor effect of succession in the next 10 years, which requires further interventions to close the recovery debt. Management adaptation modifies the biotic filter and is a crucial factor in addition to the restoration approach and the site characteristics for restoration success (Grman et al., 2013; Tölgyesi et al., 2022). For example, the introduction of sheep grazing on the experimental plots, which already exists in the surroundings, will modify the disturbance regime and improve dispersal. Overall, our results support the finding that restored dike grasslands can promote biodiversity in agricultural landscapes (Bátori et al., 2020). However, the recovery debt highlights the fact that restored grasslands cannot substitute old-growth grasslands (Nerlekar & Veldman, 2020).

AUTHOR CONTRIBUTIONS

Jakob K. Huber and Johannes Kollmann conceived the ideas and designed the experiment. Jakob K. Huber did the surveys in the years 2018–2020 and Markus Bauer in 2019 and 2021. Markus Bauer did the analyses and wrote the manuscript. Johannes Kollmann and Jakob K. Huber critically revised the manuscript and gave final approval for publication.

ACKNOWLEDGEMENTS

We would like to thank our project partners Dr. Markus Fischer, Frank Schuster and Christoph Schwahn (WIGES GmbH) as well as Stefan Radlmair and the late Klaus Rachl (Government of Lower Bavaria) for numerous discussions on restoration and management of dike grasslands. Fieldwork was supported by Clemens Berger and Uwe Kleber-Lerchbaumer (Wasserwirtschaftsamt Deggendorf). We thank Holger Paetsch, Simon Reith, Anna Ritter, Jakob Strak, Dr. Leonardo H. Teixeira and Linda Weggler for assisting with the field surveys or soil analyses in 2018–2020. The German Federal Environmental Foundation (DBU) supported MB with a doctoral scholarship. Thank you also to three anonymous referees for their valuable suggestions improving the manuscript. Open Access funding enabled and organized by Projekt DEAL.

FUNDING INFORMATION

MB was funded by a doctoral scholarship of the German Federal Environmental Foundation (DBU; No. 20021/698). The establishment of the experiment and the vegetation surveys were financed by the WIGES GmbH in the years 2018–2020 (No. 80002312).

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data and code are available via Zenodo repository doi: https://doi.org/10.5281/zenodo.7713396 (Bauer et al., 2023b). Model evaluation can also be directly accessed via GitHub: https://github.com/markus1bauer/2023_danube_dike_experiment/tree/main/markdown.

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SUPPORTING INFORMATION

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

Appendix S1. Weather and floods during study period.

Appendix S2. Designing habitat-specific species pools and seed mixtures.

Appendix S3. The community-weighted means (CWM) of plant traits of the seed mixtures.

Appendix S4. Establishment rate of sown species.

Appendix S5. All species which occurred 2018–2021 and the amount of plots in which they appeared.

How to cite this article: Bauer, M., Huber, J. K., & Kollmann, J. (2023). Fit by design: Developing seed–substrate combinations to adapt dike grasslands to microclimatic variation. *Journal of Applied Ecology*, *60*, 2413–2424. https://doi.org/10.1111/1365-2664.14497