Journal of Vegetation Science IAVS

RESEARCH ARTICLE

Beta diversity of restored river dike grasslands is strongly influenced by uncontrolled spatio-temporal variability

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Co-ordinating Editor: Jonathan Bennett

Abstract

Aims: Understanding the spatio-temporal patterns of restoration outcomes is crucial to improve predictability of restoration. High beta diversity of species-rich communities is sought because it increases overall biodiversity and improves ecosystem stability and multifunctionality. For predictive restoration, it is important to identify the significance of drivers like site characteristics but also uncontrolled factors such as spatial effects, historical factors, and year effects.

Location: Dikes at river Danube, SE Germany.

Methods: We studied dike grasslands 4–19 years after restoration over five years (2017–2021, 41 plots in 12 sites). We calculated beta diversity indices to describe spatial variation and temporal turnover, including their additive components 'replacement' and 'nestedness', or 'gains' and 'losses'. We analysed the main drivers of beta diversity like local site characteristics, landscape, and historical factors.

Results: Spatial variation of the restored dike grasslands was dominated by the replacement component and showed no homogenisation despite a significant temporal turnover. The replacement drivers changed over time, although replacement was mainly affected by slope aspect and landscape factors. Historical factors were inconsistent over time, and no statistically clear drivers of nestedness were found. The dike grasslands exhibited a year-to-year turnover in species composition of $37 \pm 11\%$. Gains and losses were balanced over time, although the ratio changed and was most pronounced on south-facing slopes.

Conclusions: The restored grasslands exhibited spatial variation by site characteristics but also by spatial factors which were not controlled by restorations. Moreover, high non-directional temporal turnover occurred, caused most likely by weather fluctuations, slightly varying management, and stochastic biotic dynamics. Thus, flexible targets are recommended for restoration monitoring, by defining a set of desired states within a certain range. Furthermore, the dominance of the replacement component of spatial variation should move the focus from defining one precise restoration approach to defining a set of possible methods which together would foster beta diversity.

1 | INTRODUCTION

The purpose of ecological restoration is to predictably restore ecosystems at the landcape scale (Brudvig, 2011). To this aim, species composition must be affected not only by manipulating local site conditions, but also by taking into account the landscape context and historical factors (Suding, 2011). However, most of the variability in restoration outcomes remains unexplained (Grman et al., 2013), and this unexplained variability in species composition is due to unmeasured deterministic factors, though it is also caused by stochastic processes (Mori et al., 2018). Stuble et al. (2017) showed that the same restoration measure carried out in different years and sites resulted in contrasting species compositions. This elusive spatio-temporal variability makes it difficult to achieve predictability, but the ensuing high beta diversity can be beneficial to overall biodiversity by preventing biotic homogenisation (Socolar et al., 2016). At the landscape scale, a high spatial beta diversity is important for ecosystem function multifunctionality (EFM, *sensu* Manning et al., 2018), and it is an insurance for ecosystem resilience (Hautier et al., 2018; Wang et al., 2021). Restoration strives for biodiversity conservation and ecosystem service multifunctionality (ESM, *sensu* Manning et al., 2018), and, as shown, high beta diversity can be useful for both. Therefore, Brudvig et al. (2017) conclude that the goal should be 'the widest possible variety of [restoration] outcomes within the range of desired conditions'.

The metacommunity concept can help to understand spatial beta diversity because it incorporates local environmental filtering and biotic interactions as well as the dispersal filter on the regional scale and ecological drift (Leibold et al., 2004), which are all necessary to guide restoration during global change (Chase et al., 2020). A promising approach to analyse spatial beta diversity, also called 'spatial variation' (Anderson et al., 2011), is its partition into two additive components, i.e., 'replacement' and 'nestedness'. Replacement is the substitution of species from one site to another by the same number of new species, while nestedness describes that species of one community are a subset of a richer one (Baselga, 2010). If replacement especially of target species dominates, conservation should protect all sites equally since all are important for biodiversity; if nestedness especially of target species dominates, conservation should focus on the most diverse site (Socolar et al., 2016), or alternatively adaptive management should reduce this richness gradient among the restored sites.

Understanding spatial variability among restoration outcomes requires identifying key drivers of community assembly (Chase et al., 2020) to assess which factors are worth manipulating, and which are important but not modifiable. This requires experiments but also learning from real-world, less standardised restoration projects at the landscape scale (Brudvig et al., 2017; Kaulfuß et al., 2022).

In semi-natural grasslands of fertile landscapes, replacement is mainly affected by local environmental factors such as soil characteristics and management, and in nutrient-poor landscapes, by uncontrolled factors, which are not modified by restoration, such as landscape configurations (Conradi et al., 2017). In addition to landscape and local factors, historical contingencies can influence species composition for a long period of time (Fukami, 2015). For restorations, this can be captured by measuring the effects of site age or weather during establishment (Grman et al., 2013), as they capture year effects with lasting consequences for species composition (Werner et al., 2020). In real-world projects, restoration measures add variability to the restoration outcomes because they are less standardised than experiments and slightly vary due to economical or practical reasons, for example, condition of donor site, timing of hay transfer, etc.

There is still a high amount of unexplained spatial variation (Grman et al., 2013; Conradi et al., 2017). This occurs due to non-directional 'baseline temporal change', which does not have to change species richness, but causes fluctuations in species composition (Blowes et al., 2019; Magurran et al., 2019). Climate change or nitrogen depositions can lead to directional trends, while weather fluctuations, irregular disturbance, dispersal, and biotic stochasticity (e.g., demographic stochasticity, biotic interactions) result in non-directional year-to-year fluctuations of species composition, also called 'year effects' (Magurran et al., 2019; Werner et al., 2020). Disturbance includes varying management since practitioners cannot guarantee to cut or graze each year at the same phenotypic stage or miss a cut due to rainy weeks. Non-directional fluctuations can exert the effects of directional trends on temporal turnover, and the strength of temporal turnover can vary in space (Fischer et al., 2020). Restoration monitoring should account for this temporal beta diversity (Hillebrand et al., 2018), also called 'temporal turnover' (Anderson et al., 2011), since it promotes biodiversity and ecosystem stability (Tredennick et al., 2017; Wang et al., 2021).

The aim of this study is to measure the importance of spatio-temporal variability on restoration outcomes in a real-world context where basically the same approach and management had been conducted. As suggested by Magurran et al. (2019), our study does frequent monitoring with plots distributed at a landscape scale. We conducted surveys for five years in 41 plots distributed on dikes along the river Danube. Thus, surveys had replicates for spatial variation and for year-to-year temporal turnover, both of which are rare in vegetation studies (Hodapp et al., 2018). Moreover, dike grasslands can combine infrastructure with biodiversity and reconcile multiple ecosystem services like dike security, conservation, recreation and biomass production (Bowman et al., 2017; Teixeira et al., 2023). These grasslands are not intensively managed and can

enrich the biodiversity of an intensively used agricultural landscape (Bátori et al., 2016; Husicka, 2003), while providing dike stability.

For this study, we asked the following questions:

1. How strong is the spatial variation and temporal turnover in species composition?
2. What is the ratio of replacement to nestedness for spatial variation, and of gains to losses for temporal turnover?
3. How much do uncontrolled spatial factors influence species composition compared to local or historical factors?

2 | MATERIALS AND METHODS

2.1 | Study area

The study was conducted on dikes along the river Danube over 63 river-km from Straubing to Vilshofen in SE Germany (Figure 1, Appendix S1; 302–318 m a.s.l.; WGS84 [lat., lon.]: 48.82903, 12.94671). The climate is temperate-suboceanic with a mean annual temperature of 8.4°C and precipitation of 984 mm (Deutscher Wetterdienst [DWD], 2021). The dikes had been constructed between 2002 and 2013 (plot age: 4–19 years), and the soil for the coverage layer was taken from the respective construction sites. Productive soils were used for waterside slopes, which promotes rapid vegetation development as necessary for erosion protection on the waterside (Kleber-Lerchbaumer et al., 2017), while less productive soils were used on the landside. The target vegetation types were calcareous grasslands (EUNIS code R1A) or lowland hay meadows (R22M; Chytrý et al., 2020, Appendix S2). The waterside was seeded with regional seed mixtures from certified producers (5–8 g m^{-2}), while on the landside threshing material (8–25 g m^{-2}) from nearby species-rich meadows was applied. For the first five

years after construction, the dikes were mown 2–3 times per year, and afterwards 1–2 times per year or grazed by sheep with a subsequent late cut. All in all, restoration and management of the dike grasslands reflected the current practice in the region.

2.2 | Species composition data

The grassland vegetation was surveyed in June or July 2017–2019 and 2021 in 41 plots (Braun-Blanquet, 1964) with a plot size of 25 m^2 (2.0 m × 12.5 m), located halfway up the slopes of the dikes on both the water- and landsides. We assigned the plots to the European habitat types (Chytrý et al., 2020) and defined specialists as species of the vegetation classes Molinio-Arrhenatheretea or Festuca-Brometea, but also of Trifolio-Geranietea, Sedo-Scleranthetea, or Nardetea strictae (Appendix S2).

All following beta diversity indices were calculated with Sørensen dissimilarities (presence–absence data). Spatial variation of species compositions was calculated for each year separately $\left(\beta_{sor} = \frac{b+c}{2a+b+c}\right)$, and was divided into its two additive components replacement $\left(\beta_{sim} = \frac{\min(b,c)}{a+\min(b,c)}\right)$ and nestedness ($\beta_{sne} = \beta_{sor} - \beta_{sim}$; Baselga, 2010), where a is the number of species occurring on both sites, b is the number of species that only occur in the first plot, and c is the number of species occurring only in the second plot. We chose Baselga's (2010) approach because it is independent of species richness for the replacement component (Baselga & Leprieur, 2015). For each year, the overall spatial variation and its components were calculated as multiple-site dissimilarity ($\beta_{SOR} = \beta_{SIM} + \beta_{SNE}$; Baselga, 2013).

Temporal aspects were expressed as the temporal beta diversity index (TBI) for which each plot was compared between consecutive years (Legendre, 2019; corresponding to species exchange ratio [SER], Hillebrand et al., 2018). This index adapted Baselga's indices to the needs of a directional character of temporal studies
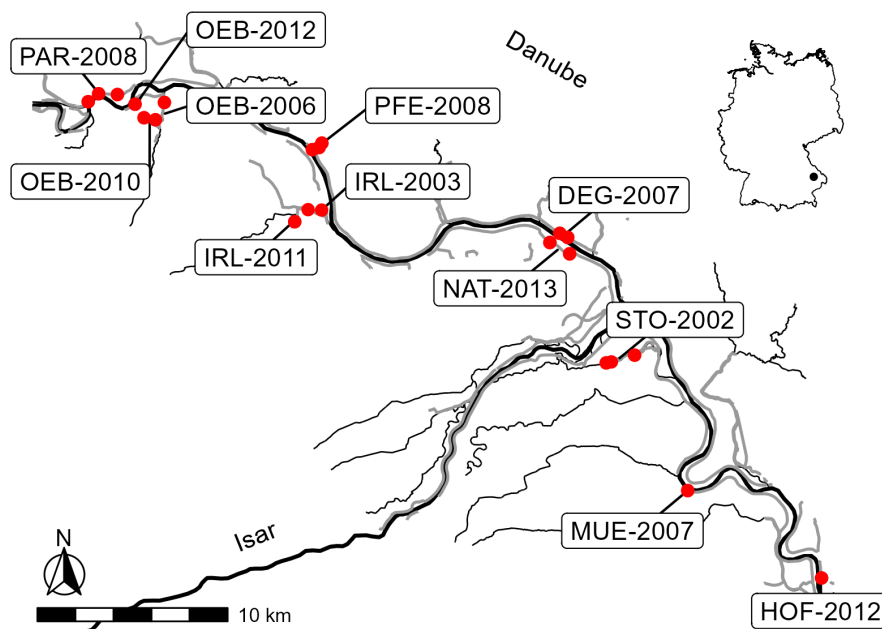

FIGURE 1 Study sites with dike grasslands along the river Danube in SE Germany. The 41 plots (red dots) were placed on dikes (grey lines) at twelve locations (labels with restoration year) along the river and its local tributaries (black lines). Data source of river courses: Bavarian State Office for the Environment, www.lfu.bayern.de.

(Legendre, 2019). The TBI ($D_{sor} = \frac{b+c}{2a+b+c}$) does not compare two plots in space but one plot over two points in time. This means that *a* is the number of species occurring at both times, *b* is the number of species that were lost, occurring only at time 1, and *c* the number of species gains, occurring only at time 2. The TBI and can be decomposed into species gains ($D_{gain} = \frac{c}{2a+b+c}$) and losses ($D_{loss} = \frac{b}{2a+b+c}$). Additionally, the abundance-based TBI (D_{bc}) was calculated with Bray–Curtis dissimilarities.

2.3 | Local, historical, space, and time variables

We measured several soil characteristics at each plot: pH, soil texture, C/N ratio, topsoil depth, $CaCO_3$, humus, nitrogen, phosphorus, potassium, and magnesium (Appendix S3). Soil sampling was conducted in August and September 2017. It would have been valuable to have soil samples from the beginning of the restorations, but all sites were restored before our monitoring started. The soil variables were scaled to unit variance and used for a principal component analysis (PCA_{soil}). $PC1_{soil}$ represented the variation from high sand to high silt proportions as well as from high C/N ratios to high amounts and concentrations of N. $PC2_{soil}$ described the variation from high amounts of phosphorus to high $CaCO_3$ proportions, while $PC3_{soil}$ mainly showed the variation in soil depth (Table 1, Appendix S4). As spatial factors, we calculated the number of semi-natural grassland biotopes (not dikes) within a radius of 500 m and the distance to the closest of those biotopes (Table 1; Bayerisches Landesamt für Umwelt [LfU], 2022).

For the analysis of spatial variation, we tested the effects of plot age and the legacy of weather conditions during the establishment phase. We used the temperature and precipitation data of the year of establishment and of the next year (Appendix S5). From monthly values, we calculated the mean averages of the year of establishment and the following year (i.e., March–February), and the average of the seasons (e.g., spring, March–May) of the year of establishment and the following year; the 20 variables were subjected to a $PCA_{climate}$ (Table 1, Appendix S5). Furthermore, we quantified spatial structures at multiple scales with distance-based Moran's eigenvector maps (dbMEM), which were based on the coordinates of the plots (Dray et al., 2006). First, the species data were Hellinger-transformed to downweigh rare species. Second, the matrices of Euclidean (geographic) distances between the plots were truncated to include only the distances of close neighbours. Third, a principal coordinate analysis (PCoA) was computed, from which six eigenvectors with positive spatial correlations were selected. The first eigenvector per year (MEM1) was correlated with river-km; therefore, it was excluded from the models. We received a MEM2 with $p < 0.05$ for 2018 and 2021, which we used as an explanatory variable because it accounts for unmeasured spatial configurations. For the analysis of temporal turnover, we included as an explanatory variable the year of dike construction combined with the location, resulting in 12 combinations.

2.4 | Data analysis

We visualise species compositions with a non-metric multidimensional scaling (NMDS) ordination and fitted environmental variables to the ordination. For the analysis of spatial variation, we used a distance-based redundancy analysis (db-RDA) with the Sørensen index and a forward selection of explanatory variables for each year and each spatial variation component (replacement and nestedness), separately. The db-RDA is an ordination method which is a multiple linear regression followed by a PCA. Forward selection was carried out with the double stopping criterion when the full model had statistically clear effects to avoid overestimation (Blanchet et al., 2008). The selection was stopped if no further variable had a statistically clear effect, or if a variable brought the model over the value of the R^2_{adj} of the global model. Afterwards, we conducted variation partitioning for each year separately to identify the main sets of drivers of the spatial variation (Peres-Neto et al., 2006), for example, the environmental, spatial, or historical set. To test if there were statistically clear effects on the species composition, we performed a partial db-RDA that controlled for the variation explained by all other variables or all other sets of variables. If $p < 0.05$, we called the effects 'statistically clear' *sensu* Dushoff et al. (2019).

To analyse the temporal turnover, the continuous variables were first scaled, centred, and checked for collinearity. Since the correlation between biotope area and distance had a Pearson $|r| > 0.7$, we excluded biotope area (Dormann et al., 2013). After modelling, we calculated the variance inflation factor (VIF) and removed variables with a VIF > 10 from the model (Table 1). If necessary, we transformed the response variables to meet the model assumptions. We calculated Bayesian linear mixed-effects models (BLMM) with the random effect 'plot' and used the restricted maximum-likelihood estimation (REML), the optimiser Nelder–Mead and, for the random effect, the Wishart prior. To identify the final model, we first reviewed the residual diagnostics of the candidate models and subsequently compared the remaining models using the Akaike information criterion adjusted for a small sample size (AICc) and chose the most parsimonious model. Finally, we calculated the marginal and conditional coefficients of determination (R^2_m, R^2_c) and the 95% confidence intervals of the response variables.

We performed all analyses in R (R Core Team, 2022), with the functions 'beta.div.comp', 'TBI' and 'forward.sel' of the package *adespatial* to calculate spatial and temporal beta diversity, and to perform forward selection (Dray et al., 2021). Habitat types were assigned to the plots with the scripts of Bruelheide et al. (2021). For NMDS, db-RDA, and variation partitioning, the functions 'metaMDS', 'envfit', 'dbrda', and 'varpart' of the package *vegan* were used (Oksanen et al., 2020); the package *blme* (based on *lme4*) for BLMM (Chung et al., 2013; Bates et al., 2015); the functions 'AICc' and 'r.squaredGLMM' of *MuMln* for the AICc estimates, and the goodness of fit evaluation with pseudo-R^2 values (Barton, 2020); and the package *DHARMa* for model evaluation (Hartig, 2021).

TABLE 1 Explanatory variables used for the full models on the temporal turnover and spatial variation of plant species on dike grasslands of the river Danube.

Variable set	Variable [unit]	Explanation	Model
Local site characteristics	$PC1_{soil}$	Sand vs nitrogen and silt	SV, TT
	$PC2_{soil}$	$CaCO_3$ vs P	SV, TT
	$PC3_{soil}$	Negatively correlated with soil depth	SV, TT
	Slope aspect	South- vs north-exposed slope	SV, TT
	Water-/Landside	Waterside vs landside slope	SV, TT
Spatial variables–Landscape context	Location × restoration year[a]	Twelve groups of plots at the same location and restored in the same year	–
	Location	Nine groups of plots at the same location	SV
	River-km [km]	Distance from the estuary measured along the river course	SV, TT
	Distance to river [m]	Orthogonal distance to the riverbed of the Danube	SV, TT
	Distance to closest biotope [m]	Orthogonal distance to the edge of the closest mapped grassland biotope	SV, TT
	Biotope area $[m^2]$[b]	Grassland habitat amount within 500-m radius	–
	MEM1[b]	Distance-based Moran's Eigenvector Maps variable 1	–
	MEM2[c]	Distance-based Moran's Eigenvector Maps variable 2	SV
Historical factors	Plot age [year]	Time since restoration	SV
	$PC1_{climate}$	High precipitation during the establishment year followed by dry summer	SV
	$PC2_{climate}$	Warm autumn during the establishment year followed by high rainfall in autumn	SV
	$PC3_{climate}$	Warm and dry summer during establishment year	SV

Note: The variables were grouped in three sets: local, spatial, and historical. PC1–PC3 are the first three axes of the principal component analyses (PCA) for soil factors (Appendix S3) and climate conditions during establishment (Appendix S4).

Abbreviations: SV, spatial variation; TT, temporal turnover.

[a]Excluded due to variance inflation factor (VIF) ≫ 10.

[b]Excluded from the final models due to the correlation with 'biotope distance' or 'river-km'.

[c]Only obtained for years 2018 and 2021.

3 | RESULTS

3.1 | Target habitat types, spatial variation and temporal turnover

The restored dike grasslands should reach an European habitat type. The NMDS show the different species compositions of the different habitat types (R1A, R22, V38; Figure 2). Per year 37%–51% of the surveyed plots were classified as the targeted habitat types of hay meadows (R22) or calcareous grasslands (R1A; Appendix S6). Continually, about half of the plots were classified as general grasslands (R, 41%–51%), and 0%–15% failed and were classified as ruderal,

dry, or anthropogenic vegetation (V38). The classification of a single plot changed partly over time (Appendix S7). Between the years there were no differences in species composition ($R^2 = 0.02$). The number of plots associated with R1A and V38 constantly increased, however, and the plots of R22 decreased during the study period. The observed vegetation showed a gradient of increasing specialist richness ($R^2 = 0.40$) with decreasing ruderal cover ($R^2 = 0.10$; Figure 2).

We were interested in the size of spatial variation between the surveyed plots and of temporal turnover of species within plots. The overall spatial variation in species composition among the dike grasslands was constant over the years ($\beta_{SOR} = 0.32$–0.34); it was always dominated by replacement ($\beta_{SIM} = 0.28$–0.29) and never by
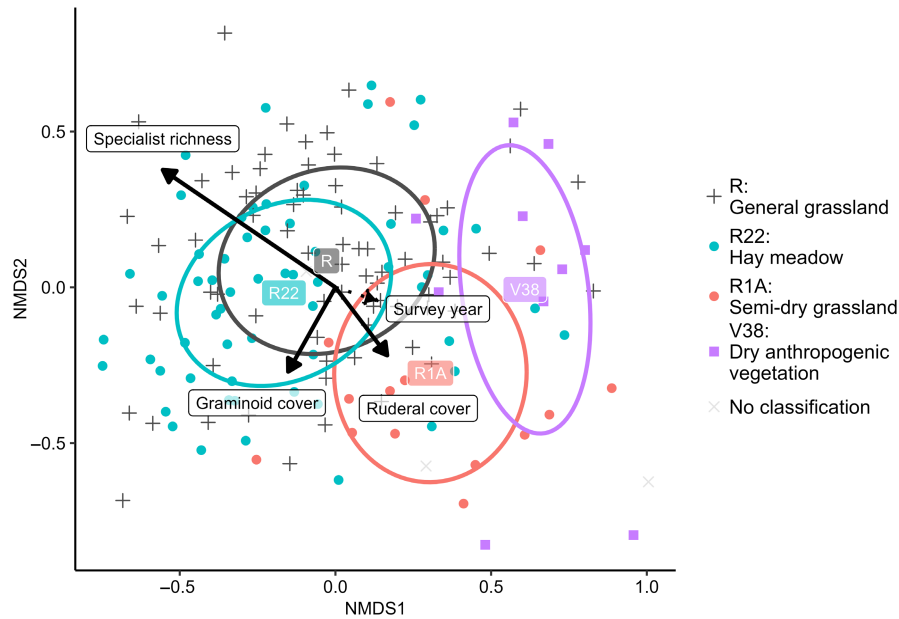
FIGURE 2 NMDS ordination based on Sørensen dissimilarity of the species compositions of 164 dike plot surveys. The 41 plots were surveyed 2017–2021 on dikes of the river Danube. The colours indicate the habitat type of the plot (*sensu* Chytrý et al., 2020; $R^2 = 0.19$; Appendix S6). The vectors indicate the gradients specialist richness vs ruderal cover ($R^2 = 0.45$; $R^2 = 0.10$) and graminoid cover ($R^2 = 0.08$). The survey year was not statistically clear ($R^2 = 0.02$). The circles show the standard error (SE) of the vegetation classes. 2D stress: 0.25.
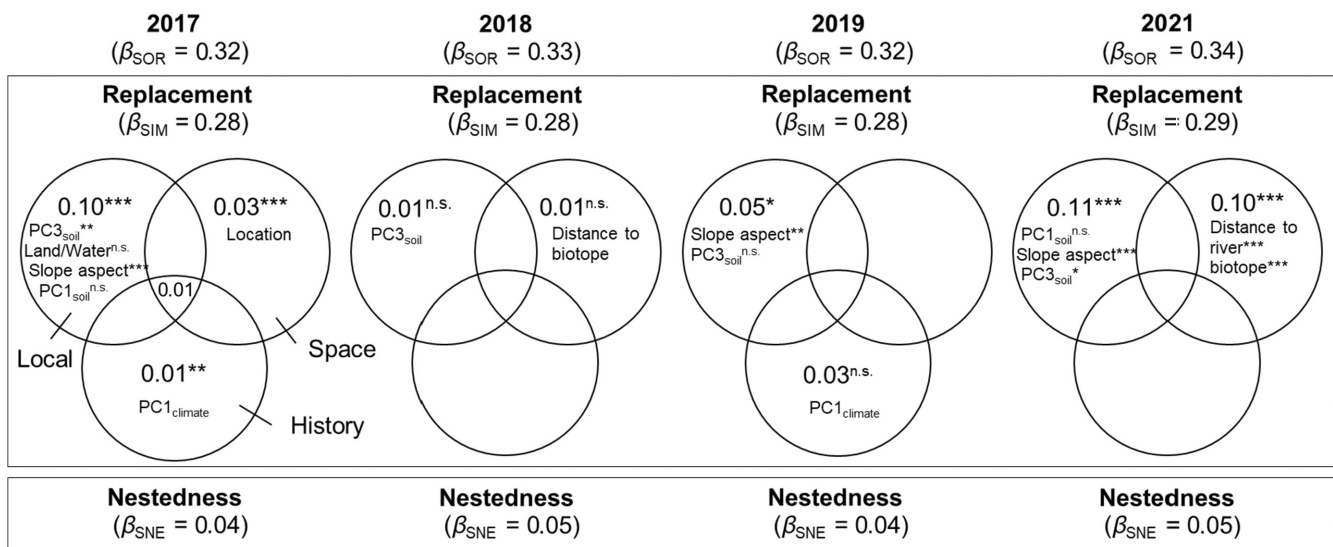

FIGURE 3 Spatial variation in species composition among dike grasslands along the river Danube. The overall spatial variation (β_{SOR}) and its components, replacement (β_{SIM}) and nestedness (β_{SNE}) are shown. For the replacement-driven dissimilarity, the results of the variation partitioning are shown, and the pure and combined contributions (ratios 0–1) of each variable set: local environmental, spatial, and historical factors (Table 1). The variables presented were obtained by forward selection and sorted from high to low (partial) R^2 values. The P values were calculated for the entire set of variables and single variables by partial distance-based redundancy analysis (db-RDA). ***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$; ns, not statistically clear; Land/Water, landside/waterside; PC_{soil}, eigenvectors of a Principal Component Analysis (PCA) of soil variables; $PC_{climate}$, eigenvectors of a PCA of climate variables during the establishment of the dike grasslands; Distance to biotope, distance to the closest mapped grassland biotope which is not a dike.

nestedness ($\beta_{SNE} = 0.04$–0.05; Figure 3). The temporal turnover per plot was $37 \pm 11\%$ (mean ± SD), and the colonisations and local extinctions were balanced over time ($-3 \pm 16\%$; Figure 4); this was reflected by the subset of specialist species (Appendix S8).

3.2 | Drivers of beta diversity

Which drivers affected spatial variation between the restored sites? For the replacement component (β_{sim}), the measured
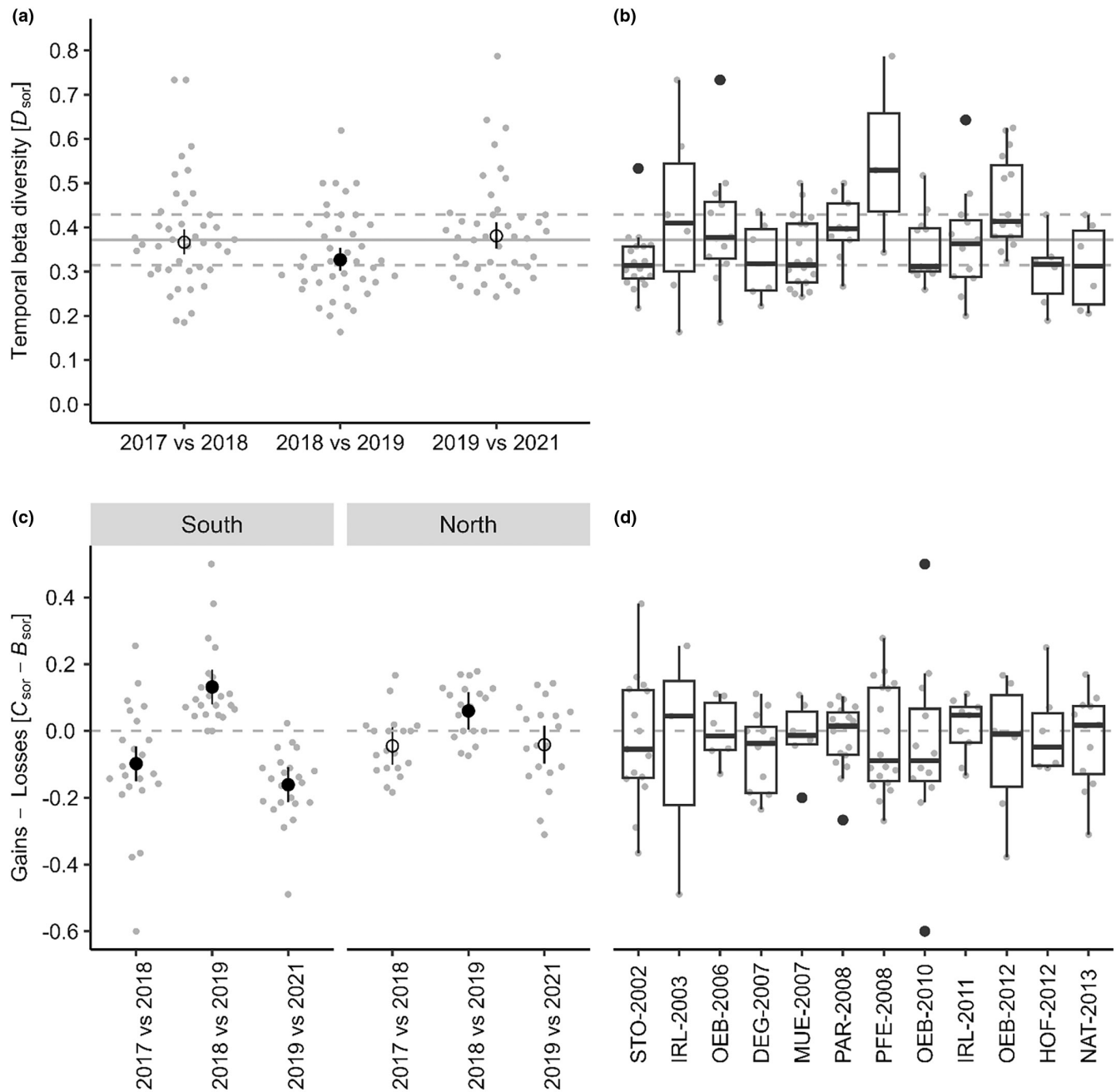
FIGURE 4 Year-to-year turnover analysed by calculating the temporal beta-diversity index (TBI), including 41 plots over four years with presence–absence data based on Sørensen dissimilarity (D_{sor}) (a,b). Furthermore, the two components of TBI are compared, that is, gains (C_{sor}) and losses (B_{sor}) (c,d). Turnover was analyzed over time (a,c), and at certain locations which are subdivided by restoration year (b,d). For values of covariables, see Appendix S9. The black dots show the estimates accompanied by their 95% confidence interval (CI95) obtained from a Bayesian linear mixed-effects model (BLMM). The grey dots are the raw data, and the grey horizontal lines show the overall mean and standard deviation (a,b) or mark the balance between gains and losses (c,d). The black dots are filled if their CI95 does not cross the overall mean of the raw data or the 0 line; the locations are sorted by construction year. $R_m^2 = 0.28$ and $R_c^2 = 0.42$ (a); $R_m^2 = 0.41$ and $R_c^2 = 0.42$ (c). The locations were not included in the model because of a high variance inflation factor (Table 1). The boxplots show the median and the first and third quartiles.

variables explained more of the replacement-driven dissimilarity in 2017 and 2021 (0.15–0.21) than in the years 2018 and 2019 (0.02–0.08). The local site characteristics changed species composition over the four years (Figure 3). Furthermore, the site characteristics always explained slightly more of the variation than the other sets of variables (1%–11%). Spatial factors had an effect in

three years and explained 1%–10%, while historical factors were only included in two years (1%–3%).

Slope aspect was a driver of replacement-driven dissimilarity (β_{sim}) in three years ($F_{1,37} > 3.0$, $p < 3.4e{-}03$; Figure 3). The substrate depth (PC3$_{soil}$) influenced the replacement component in all four years but was statistically clear only in 2017 and 2021 ($F_{1,27} > 2.2$,

$p < 2.8e{-}02$). Location was a statistical clear driver in 2017 ($F_{8,27} = 3.0$, $p = 1.0e{-}04$), and in 2021 the distance to the river and to the closest biotope ($F_{1,35} > 3.2$, $p < 8.0e{-}04$). High rainfall during the establishment year ($PC1_{climate}$) had a clear effect in 2017 ($F_{1,27} = 3.4$, $p = 2.4e{-}03$; 2019: $F_{1,27} = 1.9$, $p = 5.5e{-}02$), while no statistically clear driver was found for nestedness (β_{sne}).

Temporal turnover is a significant factor in plant communities, but is it constant and do gains or losses prevail? Year-to-year temporal turnover was lower between 2018 and 2019 compared to 2017/2018 and 2019/2021 (Figure 4a; final model, $R^2_m = 0.28$ and $R^2_c = 0.42$). The differences between the 12 locations were larger than those between years, but the uncertainty within the locations was far higher than the differences between the locations (Figure 4b). The ratio of species gains to losses was inconsistent over the years. Between 2018 and 2019, the plots gained species, while between 2017/2018 and 2019/2021, the plots predominantly lost species. This pattern was clearest on the south-exposed plots (Figure 4c; final model, $R^2_m = 0.41$ and $R^2_c = 0.42$). At no location did gains or losses dominate over the three comparisons (Figure 4d).

4 | DISCUSSION

Many dike grassland plots along the river Danube reached the desired habitat types, but the number varied over time, and some plots developed to a ruderal habitat type. The spatial variation was mainly driven by replacement, and the important drivers were spatial factors and slope aspect. No homogenisation of overall spatial variation was observed over the four observed years despite a large year-to-year species turnover. The turnover was constantly high but varied in its intensity from year to year, though the ratio between gains and losses was balanced.

4.1 | High temporal turnover and spatial variation in restoration outcomes

For practitioners and restoration ecologists, it is important to know the strength of spatial variation by uncontrolled factors at the landscape scale, to recognise that there is temporal turnover and to quantify this turnover. The total spatial variation ($\beta_{SOR} = 32\%$–34%) in restored dike grasslands did not show a tendency of homogenisation in the years 2017–2021 (41 plots of 25 m²; Figure 3), but was lower than the spatial variation in semi-natural grasslands in Germany and Great Britain observed by Diekmann et al. (2019) (67%–75%, 36–82 plots of approximately 25 m²). This could be due to a lack of rare species that drive spatial variation based on presence–absence data (Mori et al., 2018), but also due to the use of species-rich and regional (standardised) seed mixtures that can lead to biotic homogenisation through restoration (Holl et al., 2022).

We observed year-to-year turnover rates of 22%–59% (5%–95% quantiles; median 36%; Figure 4) in the restored dike grasslands. This was a smaller variation but a similar median, compared with a global grassland experiment in its first five years (12%–86%; Hodapp et al., 2018), other local grassland experiments measured over 3–11 years (ca. 30%; Eckhoff et al., 2023) and global grasslands measured over 1–8 years within a range of 10%–70% (5%–95% quantiles; median ca. 39%; Hillebrand et al., 2018). Furthermore, Diekmann et al. (2019) observed long-term changes in grasslands of 46%–77%. These comparisons suggest that short-term turnover in grasslands was not necessarily less intense than mid-term turnover. Temporal turnover caused mainly non-directional fluctuations but also a slight directional change (Appendix S10), which indicates that the grasslands are changing or still developing after 4–19 years. For our surveyed grasslands, baseline change is more important than directional change, which shifts the focus to non-directional drivers of turnover like weather, demographic, or management fluctuations (Magurran et al., 2019; Werner et al., 2020). For restoration, baseline change can be beneficial since it enables coexistence (Chesson, 2000), while it requires a greater effort for restoration evaluation since monitoring needs more than one year to assess restoration outcomes. This baseline change but also the observer error, which is always included, challenge predictive restoration (Morrison, 2016; Brudvig et al., 2017).

4.2 | Dominance of replacement and balanced temporal turnover

Restoration aims for a balanced temporal turnover and a replacement-driven spatial variation to avoid homogenisation and to foster biodiversity at all sites (Socolar et al., 2016). Here, spatial variation was mainly replacement-driven (27%–29% vs 4%–5%; Figure 3), which is in line with other local and global studies (Conradi et al., 2017; Soininen et al., 2018; Diekmann et al., 2019). The observed low nestedness component was similar to that of Conradi et al. (2017), but only to certain studies analysed by Diekmann et al. (2019), who calculated values in the range of 5%–19%. The low nestedness suggests that most absent plant species are substituted at another site by other species. Gains and losses dominated in different years, but were balanced over the entire study period and for every location (Figure 4), similar to a global study with time series over 10 years (Dornelas et al., 2019). The same applies to the subset of specialist species, which indicates that an undesired change from meadow species to ruderals is not the case (Appendix S8).

4.3 | Responses of communities to space, time, and local site characteristics

To understand the mechanisms behind patterns of beta diversity, it is necessary to know the main drivers of (meta)community assembly (Chase et al., 2020). For spatial variation in species composition, we only identified statistically clear drivers for replacement but not for nestedness, similar to another study in calcareous grasslands (Conradi et al., 2017) probably due to the low ratio of nestedness.

For replacement, we discovered as main drivers local factors followed by spatial factors, which is in accordance with other studies (Grman et al., 2013; Conradi et al., 2017, but see Bagaria et al., 2019). However, the main drivers varied over time, indicating that the drivers of spatial variation can change in strength from year to year. The fact that historical factors were only relevant in 2017 and 2019 is not very reliable, as historical contingencies would logically have to persist or eventually disappear. Besides, the accumulated variables explained less of the spatial variation during the two dry years 2018 (2%) and 2019 (8%; Hari et al., 2020; Appendix S11) compared to 2017 (15%) and 2021 (21%). This suggests a greater relative importance of temporal turnover during these dry years for species composition. It could be that ruderal species increased in these years. Such species are less dependent on constant factors which are relevant for spatial variation, but more on disturbances which provide more regeneration gaps. Our results highlight the importance of temporal replication of spatial studies to avoid misleading evidence and to improve the assumptions of uncertainty for prediction in restoration ecology.

Main local factors explaining spatial variation were slope aspect followed by substrate depth ($PC3_{soil}$), as observed in other studies (Dornbush & Wilsey, 2010; Mazalla et al., 2022). Since the replacement component dominates, the result suggests that different slope aspects and substrate depths corresponded to different species compositions, but did not cause a richness difference. This changes the discussion about the right substrate depth among practitioners (Kleber-Lerchbaumer et al., 2017) to a call for varying substrate depths on dike grasslands to foster biodiversity. We found no historical contingencies using the climate during the establishment phase, and we detected no succession effect via plot age (4–19 years) on the replacement component. That is in contrast with the results of other studies (e.g., Grman et al., 2013), but fits the low directional temporal turnover in our study. However, we observed a site effect in three out of four years, similar to other studies (Stuble et al., 2017). In 2017, location had an effect that integrates unmeasured factors, which may represent management regimes or landscape structures. The factor landscape structures is improbable because (i) of the use of MEMs to account for landscape effects, and (ii) for instance Grman et al. (2013) found only minor landscape effects. The factor management was intended to be generally similar for all sites. However, it could be the reason for the detected effect of location, as cutting and grazing may have varied in 2017 and for some locations, due to weather conditions, organisational or economic reasons. Especially in 2021, the distance to the river and the next seminatural grassland biotope excluding the dikes itself had an influence on spatial variation. This suggests that different degrees of connectivity result in changes in species composition in some years.

The intensity of the temporal turnover varied over time. In particular, between the two dry and hot years (2018 and 2019; Hari et al., 2020, Appendix S11), the turnover rate was reduced, which could be due to reduced biotic interactions under severe drought (Ploughe et al., 2019). The locations had different turnover intensities as in Fischer et al. (2020), although there was no evidence for a plot age effect, which is consistent with a global study by Blowes et al. (2019). Gains and losses alternated in dominance, which was particularly evident in southern-facing slopes. Interestingly, from a normal year to a dry year and the other way around (2017/18, 2019/21), losses dominated and between two dry years (2018/19), gains dominated, suggesting a drought effect (cf. Stuble et al., 2017). Droughts can cause local extinctions of low-abundance species, leading to losses (Chelli et al., 2019). The dominance of gains between two dry years might be due to reduced competition (Ploughe et al., 2019). With increasing competition, ruderal species will most likely disappear again.

5 | CONCLUSION

Biodiversity depends not only on local site characteristics or historical contingencies, but also on uncontrolled spatio-temporal dynamics (Leibold et al., 2004; Tredennick et al., 2017), which does not only include environmental factors such as climate, but also unpredictable variability in restoration and management due to practical and economic reasons (e.g., two or three cuts; timing). Therefore, spatial beta diversity on a landscape scale should be included in the evaluation of restoration outcomes and must be monitored more than once. We showed that spatial beta diversity was mainly replacement-driven, and year-to-year temporal turnover was balanced and exceeded directional development by far. These results highlight the need for defining target area for a range of tolerable outcomes instead of a certain reference point (Hobbs, 2007; Brudvig & Catano, 2021), for example, in an ordination or a certain state of a certain biotope. This means that reference data should be spatially more diverse and repeatedly surveyed to capture variation and baseline turnover (Shackelford et al., 2021). All in all, restorations should still focus on a high accuracy of restoration outcomes, but their precision (i.e., the degree of variability) should be intermediate to foster heterogeneity and avoid biotic homogenisation (Hiers et al., 2016).

To combat biotic homogenisation, we would support an even higher spatial variation than 32%–34% to increase ecosystem function multifunctionality (EFM) and ecosystem stability during environmental change (Hautier et al., 2018; Wang et al., 2021). This could be achieved by varying factors instead of searching the perfect fit, for example, by spatio-temporally complex management (Vadász et al., 2016), varied substrate depths or seed mixtures based on a random sample of a species pool albeit stratified by traits (cf. Bauer et al., 2022).

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Zenodo at https://zenodo.org/doi/10.5281/zenodo.6107806 (Bauer et al., 2024) and on GitHub with Markdown documents of model checks to scroll through: https://github.com/markus1bauer/2023_danube_dike_survey.

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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. Interactive map of the dike grasslands.

Appendix S2. Target vegetation and specialist species.

Appendix S3. Soil measurements.

Appendix S4. Table of Principal Component Analysis (PCA) of soil samples.

Appendix S5. Table of Principal Component Analysis (PCA) of climate data during grassland establishment.

Appendix S6. Table of habitat classes.

Appendix S7. Figure of temporal change of habitat types.

Appendix S8. Figure of temporal turnover calculated only with specialist species.

Appendix S9. Covariables of Figure 4.

Appendix S10. Figure of directional development 2017–2021.

Appendix S11. Table about climate and floods.

Appendix S12. Bivariate plot of temporal beta-diversity index (TBI; $D_{sor} \sim D_{bc}$) in the dike grasslands.