Research article

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

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Abstract

1. Spatio-temporal dynamics of biodiversity are a key measure when monitoring restoration success. Balanced species turnover is aimed at because it increases overall biodiversity and improves ecosystem stability and multifunctionality. For predictive restoration, it is important to analyse spatial beta diversity and to identify its drivers like site characteristics but also uncontrolled factors like spatial effects, historical factors, year effects and non-directional temporal turnover.
2. We studied dike grasslands 4–19 years after restoration at River Danube in SE Germany 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’.
3. The analysis of the spatial variation of the restored dike grasslands did not reveal homogenisation despite a significant temporal turnover, and was largely dominated by replacement-driven dissimilarity. The replacement drivers changed over time, although replacement was mainly affected by exposition and spatial factors. Historical factors were inconsistent over time, and no statistically clear drivers were found for nestedness.
4. The dike grasslands exhibited on average 37 ± 11% (mean ± SD) year-to-year turnover in species composition, with some spatio-temporal variation. Gains and losses were balanced over time, although prevalences changed over time and were most pronounced on south-exposed slopes.
5. The restored grasslands exhibited spatial variation by site characteristics but also uncontrolled spatial factors. Moreover, high non-directional temporal turnover caused by weather fluctuations, slightly varying management, and stochastic biotic dynamics influenced spatial variation. Thus, restoration targets should be defined as a desired variation of alternative states. Furthermore, the dominance of replacement should move the focus from searching the perfect fit for certain targets to a variation of the approaches to increase beta diversity.

Keywords

Community assembly

Embankment

Replacement

Spatial heterogeneity

Species composition

Temporal variability

Year effects

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, Bassett, & Brudvig, 2013). Unexplained variability in species composition includes unmeasured deterministic factors, though it is also caused by stochastic processes (Mori, Isbell, & Seidl, 2018). Stuble, Fick, and Young (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, Gilroy, Kunin, & Edwards, 2016). Moreover, a high spatial beta diversity is important for landscape-scale ecosystem function multifunctionality (EFM, sensu Manning et al., 2018), and it is an insurance for ecosystem stability (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’.

A promising approach to analyse spatial variability of species composition is the partition of spatial beta diversity, also called ‘spatial variation’ (Anderson et al., 2011), into its 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 dominates, conservation should protect the sites equally since all are important for biodiversity; if nestedness dominates, conservation should focus on the most diverse site (Socolar et al., 2016), or adaptive management should reduce this richness gradient among the restored sites.

Understanding spatial variability among restoration outcomes requires identifying key drivers to assess which factors are worth manipulating and which are important but not modifiable. This requires experiments but also learning from real-world, less standardized restoration projects at the landscape scale

(Brudvig et al., 2017; Kaulfuß, Rosbakh, & Reisch, 2022). In (semi)natural grasslands of fertile landscapes, replacement is mainly affected by local environmental factors such as soil characteristics and management, and by uncontrolled factors such as landscape configurations in nutrient-poor landscapes (Conradi, Temperton, & Kollmann, 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, Stuble, Groves, & Young, 2020). In real-world projects, restoration measures add variability to the restoration outcomes because they are less standardized than experiments and slightly vary due to economical or practical reasons, e.g., condition of donor site, date of hay transfer etc.

However, there is still a high amount of unexplained spatial variation (Conradi et al., 2017; Grman et al., 2013). This occurs due to non-directional ‘baseline temporal change’, which do not have to change species richness, but cause shifts or fluctuations in species composition (Blowes et al., 2019; Magurran, Dornelas, Moyes, & Henderson, 2019). 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, Adler, & Adler, 2017; Wang et al., 2021). 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. Fluctuations can exert higher effects on temporal turnover than directional trends (Fischer, Chytrý, Těšitel, Danihelka, & Chytrý, 2020), and the strength of temporal turnover can vary in space (Fischer et al., 2020).

The aim of the 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 was conducted. As required (Magurran et al., 2019), our study does frequent monitoring with plots distributed at a landscape scale. We conducted surveys for 5 years in 41 plots distributed on dikes along the river Danube. We observed spatial variation over time and had replicates for year-to-year temporal turnover, both of which are rare in vegetation studies (Hodapp et al., 2018). Moreover, dike grasslands are a perfect case for 'renewal ecology' since they can reconcile multiple ecosystem services (Bowman et al., 2017; Teixeira, Bauer, Moosner, & Kollmann, 2023): dike grasslands are not intensively managed and can enrich the biodiversity of an intensively used agricultural land (Bátori et al., 2016), 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 and of gains to losses?
3. How strongly do uncontrolled spatial factors influence species composition?

2 Material 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 (Fig. 1, Appendix A1; 302–318 m asl; 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 were constructed between 2002 and 2013 (plot age: 4–19 years). Productive soils were used for waterside slopes and less productive soils on the landside, which promotes rapid vegetation development for erosion protection on the waterside (Kleber-Lerchbaumer, Berger, & Veit, 2017). The target vegetation types were calcareous grasslands and lowland hay meadows (Appendix A2). The water side was seeded with regional seed mixtures from certified producers (5–8 g m^{-2}), on the landside, threshing material (8–25 g m^{-2}) was applied. Threshing material was gained from nearby species-rich meadows and soil for the coverage layer of the dikes was taken from the respective construction site. For the first five years, dikes were mown 2–3 times per year, and afterwards mown 1–2 times per year or grazed by sheep with a subsequent late cut. All in all, restoration and management reflected the current practice in the region.

2.2 Species data

Vegetation was surveyed in June or July 2017–2019 and 2021 in 41 plots (Braun-Blanquet, 1928/1964) with a plot size of 25 m² (2.0 m × 12.5 m) placed halfway up the slopes of the dike. We assigned the plots to the European habitat types (Chytrý et al., 2020) and selected reference plots of semi-natural grasslands within Bavaria from sPlotOpen (Sabatini et al., 2021). We chose four lowland hay meadow plots (EUNIS code R22; Chytrý et al., 2020) and four calcareous grassland plots (R1A) that were surveyed 1978–1991 (Appendix A2). We defined specialists as species of Molinio-Arrhenatheretea or Festuca-Brometea, but also of Trifolio-Geranietea, Sedo-Scleranthetea, or Nardetea strictae (Appendix A2).

All following beta diversity indices were calculated with Sørensen dissimilarities. Spatial variation of species compositions was calculated for each year separately (β_{sor}), and was divided into its two additive components replacement (β_{sim}) and nestedness (β_{sne}; Baselga, 2010). 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 (Legendre, 2019). The TBI (D_{sor}) compares one plot over time and can be decomposed into species gains (D_{gain}) and losses (D_{loss}). 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 (Appendix A4). Soil sampling was conducted in August and September 2017. 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 N amounts and concentrations. $PC2_{soil}$ described the variation from high phosphorus amounts to high $CaCO_3$ proportions, while $PC3_{soil}$ mainly showed the variation in soil depth (Table 1, Appendix A5). As spatial factors, we calculated the amount of semi-natural grassland biotopes (not dikes) within a radius of 500 m and the distance to the closest of that biotopes (Table 1; Bayerisches Landesamt für Umwelt [LfU], 2022).

For the analysis of spatial variation, we tested the plot age and the legacy effects by weather conditions during the establishment phase as historical factors. We used the temperature and precipitation data of the year of establishment and of the next year (Appendix A6). 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 A6). 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, Legendre, & Peres-Neto, 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 kilometres; 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 twelve combinations.

2.4 Data analysis

We visualise beta diversity with a non-metric multidimensional scaling (NMDS) ordination. For the analysis of spatial variation, we used a distance-based redundancy analysis (db-RDA) with a forward selection of explanatory variables for each year and each spatial variation component (replacement and nestedness), separately. Forward selection was carried out with the double stopping criterion when the full model had statistically clear effects (Blanchet, Legendre, & Borcard, 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 to identify the main sets of drivers of the spatial variation (Peres-Neto, Legendre, Dray, & Borcard, 2006), e.g., 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, Kain, and Bolker (2019).

To analyse the temporal turnover, the continuous variables were first scaled and centred and checked for collinearity. If the correlation exceeded a Pearson $|r| > 0.7$, we excluded one variable (Dormann et al., 2013). After modelling, we calculated the variance inflation factor (VIF) and removed variables with a VIF

> 10 from the model. 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 selections (Dray et al., 2021). Habitat types were assigned to the plots with the scripts of Bruelheide, Tichý, Chytrý, and Jansen (2021). For NMDS, db-RDA and variation partitioning, ‘metaMDS’, ‘envfit’, ‘dbrda’ and ‘varpart’ of ‘vegan’ were used (Oksanen et al., 2020); ‘blme’ (based on ‘lme4’) for BLMM (Bates, Mächler, Bolker, & Walker, 2015; Chung, Rabe-Hesketh, Dorie, Gelman, & Liu, 2013); ‘AICc’ and ‘r.squaredGLMM’ of ‘MuMIn’ for the AICc estimates and the goodness of fit evaluation with pseudo-R^2 values (Barton, 2020); and ‘DHARMa’ for model evaluation (Hartig, 2021).

3 Results

3.1 Beta diversity and habitat types

The NMDS showed that the dike grasslands were close to the historic references but hardly reacedh them (Fig. 2). However, 37–51% of the 41 plots were classified as the targeted habitat types of hay meadows (R22) or calcareous grasslands (R1A; Appendix A7). Continually, about half of the plots were classified as general grasslands (R, 41–51%), and 0–15% failed and were classified as ruderal, dry and anthropogenic vegetation (V38). The number of plots associated with R1A and V38 constantly increased, but 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 ($R^2 = 0.10$; Fig. 2).

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 nestedness ($\beta_{SNE} = 0.04–0.05$; Fig. 3). The temporal turnover per plot was 37 ± 11% (mean ± SD), and the colonisations and local extinctions were balanced over time (−3 ± 16%; Fig. 4). That was reflected in the calculation with the subset of specialist species (Appendix A10).

3.2 Drivers of beta diversity

For the replacement component (β_{sim}), the measured 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 4 years (Fig. 3). Furthermore, the site characteristics always explained slightly more of the variation then the other sets of variables (1–11%). Spatial factors had an effect in 3 years and explained 1–10% and historical factors were only included in 2 years (1–3%).

Exposition was a driver of replacement-driven dissimilarity (β_{sim}) in 3 years ($F_{1,37} > 3.0$, $p < 3.4\text{e}{-03}$; Fig. 3). The substrate depth ($PC3_{soil}$) influenced the replacement component in all 4 years, but was statistically clear only in 2017 and 2021 ($F_{1,27} > 2.2$, $p < 2.8\text{e}{-02}$). Location was a statistical clear driver in 2017 ($F_{8,27} = 3.0$, $p = 1.0\text{e}{-04}$) and in 2021 the distance to the river and to the closest biotope ($F_{1,35} > 3.2$, p

$< 8.0\text{e}{-04}$). High rainfall during the establishment year (PC1$_{\text{climate}}$) had a clear effect in 2017 ($F_{1,27} = 3.4$, $p = 2.4\text{e}{-03}$; 2019: $F_{1,27} = 1.9$, $p = 5.5\text{e}{-02}$), while no statistically clear driver was found for nestedness (β_{sne}).

Year-to-year temporal turnover was lower between 2018 and 2019 compared to 2017/2018 and 2019/2021 (Fig. 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 (Fig. 4B). The ratio of species gained to lost species 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 (Fig. 4C; final model, $R^2_m = 0.41$ and $R^2_c = 0.42$). At no location, gains or losses seems to dominate over the three comparisons (Fig. 4D).

4 Discussion

Many dike grassland plots on 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 exposition. No homogenisation was observed over the years albeit a large year-to-year species turnover. The turnover was constantly high but varied in its intensity over time, though the ratio between gains and losses was balanced out.

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 landscape scale, to recognize that there is temporal turnover and to quantify this turnover. The total spatial variation (β_{SOR} = 32–34%) in restored dike grasslands did not show a tendency of homogenisation in the years 2017–2021 (41 plots of 25 m², Fig. 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 but standardised seed mixtures that can lead to biotic homogenisation through restoration (Holl, Luong, & Brancalion, 2022).

We observed year-to-year turnover rates of 22–59% (5–95% quantiles; median 36%; Fig. 4) in the restored dike grasslands. This was a smaller variation but a similar median, compared with a global grassland experiment (12–86%; Hodapp et al., 2018), and other 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 A9), 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 can enable coexistence (Chesson, 2000), but it requires a greater afford 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 (Brudvig et al., 2017; Morrison, 2016).

4.2 Dominance of replacement and balanced temporal turnover

Restoration aims towards 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%; Fig. 3), which is in line with other local and global studies (Conradi et al., 2017; Diekmann et al., 2019). The observed low nestedness component was similar to that of Conradi et al. (2017), but only to certain studies analyzed 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, indicating that the conservation value based on species richness was generally similar for all sites. Gains and losses became dominant in different years, but over the entire study period and for every location, gains and losses were balanced (Fig. 4), similar to a global study with time series over 10 years (Dornelas et al., 2019). The same is applies to the subset of specialist species, which indicates that an undesired change from meadow species to ruderals is not the case (Appendix A10).

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 its main drivers. 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). For replacement, we discovered as main drivers local factors followed by spatial factors which is in accordance with other studies (Conradi et al., 2017; Grman et al., 2013; but see Bagaria, Rodà, & Pino, 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 tested variables explained together less of the spatial variation during the two dry years 2018 and 2019 (Hari, Rakovec, Markonis, Hanel, & Kumar, 2020) which suggests a greater relative importance of temporal turnover during these years. 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 exposition followed by substrate depth ($PC3_{soil}$). This result suggests that different expositions 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 could not identify historical contingencies using the climate during the establishment phase, and we could not identify a succession effect via plot age (4–19 years) on the replacement component. That contrasts 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 which integrates unmeasured factors, which may represent management regimes or landscape structures. The last one 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. Although management was intended to be generally similar for all sites, it could be the reason for this effect: the cutting and grazing could 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 semi-natural grassland biotope excluding the dikes itself had an influence on spatial variation. This suggests that different degrees of connectivity results in different species compositions in some years.

The intensity of the temporal turnover varied over time. In particular, between the two dry and hot years (2018/2019; Hari et al., 2020, Appendix A3), 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 similar to 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 the south exposition. Interestingly, from a normal year to a dry year and the other way around (17/18, 19/21), losses dominated and between two dry years (18/19), gains dominated, suggesting a drought effect (cf. Stuble et al., 2017). Droughts can cause local extinctions of rare 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, these specialists might disappear again.

5 Conclusion

Biodiversity depends not only on local site characteristics or historical contingencies, but also on uncontrolled spatio-temporal dynamics (Tredennick et al., 2017), which does not only include environmental factors such as climate, but also slight, unpredictable variability in restoration and management due to practical and economic reasons. 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 oucomes instead of a certain reference point, e.g., 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, Dudney, Stueber, Temperton, & Suding, 2021). All in all, restorations should still focus on a high accuracy of restoration outcomes, but their precision (variability) should and could be intermediate to foster heterogeneity (Brudvig et al., 2017).

To combat biotic homogenization, we would support an even higher spatial variation than 32–34% and 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, e.g., spatio-temporal complex management (Vadász, Máté, Kun, & Vadász-Besnyői, 2016) varying substrate depths or using seed mixtures based on a random sample of a target species pool for each location but stratified by traits (cf. Bauer, Krause, Heizinger, & Kollmann, 2022). In the future, the link of beta diversity with ecosystem service multifunctionality (sensu Manning et al., 2018) has to be further investigated.

Further information

Authors' contribution

JH and JK designed the study. JH conducted the surveys in the years 2017–2019 and MB in 2021. JH collected the soil samples. MB did the analyses and wrote the manuscript. JK and JH critically reviewed the manuscript.

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Data and code availability

https://github.com/markus1bauer/2023_danube_dike_survey

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Tables

Table 1

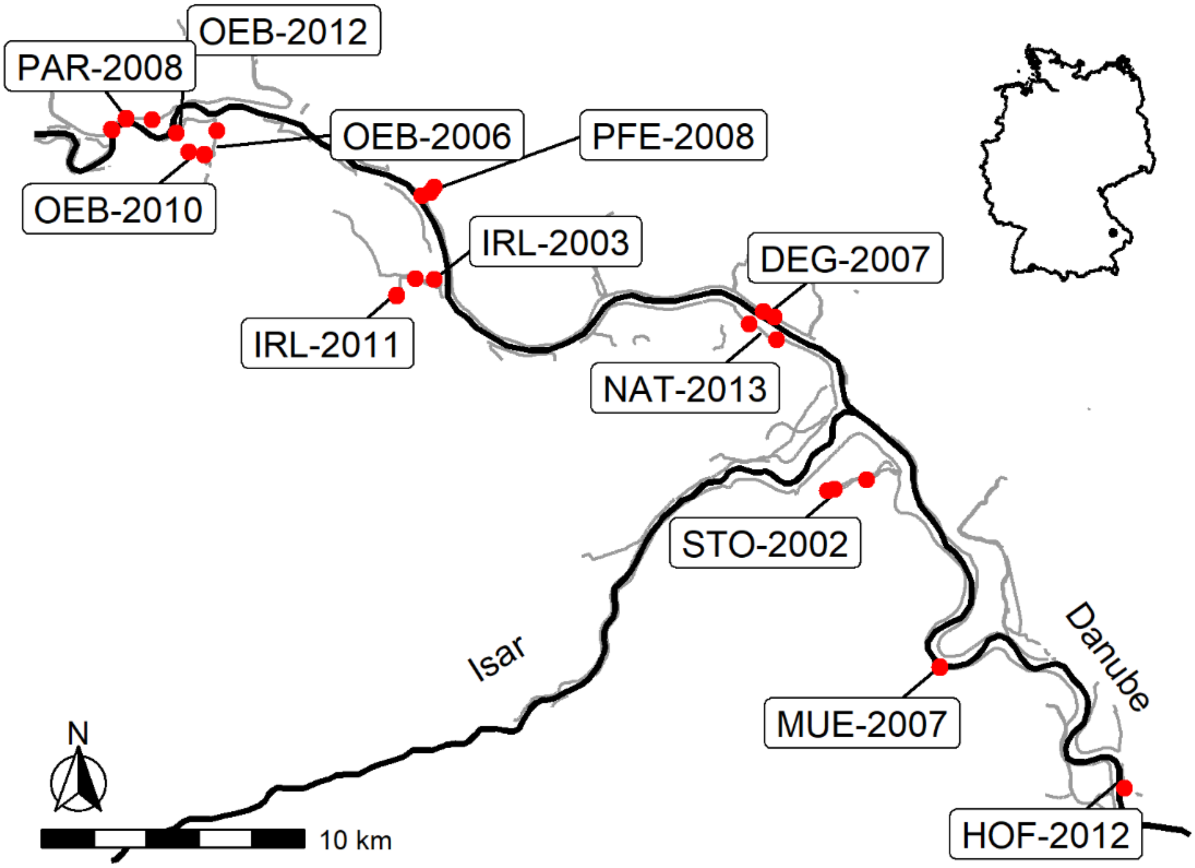
Explanatory variables used for the full models on the temporal turnover and spatial variation of plant species on dike grasslands of River Danube. The variables were grouped in three sets: local, spatial, and historical. PC1–PC3 are the first three axes of the principal component analyses (PCA) for soil factors (Appendix A4) and climate conditions during establishment (Appendix A5). TT = temporal turnover; SV = spatial variation; * excluded due to variance inflation factor (VIF) ≫ 10; ** excluded from the final models due to the correlation with 'biotope distance' and 'river km'; *** only obtained for years 2018 and 2021.

Variable set	**Variable [unit]**	**Explanation**	**Model**
Local site characteristics	$PC1_{soil}$	Sand vs. nitrogen/silt	Both
	$PC2_{soil}$	$CaCO_3$ vs P	Both
	$PC3_{soil}$	Negatively correlated with soil depth	Both
	Exposition	South- vs. north-exposed slope	Both
	Water-/Landside	Waterside vs landside slope	Both
Spatial variables–Landscape context	Location x restoration year*	12 groups of plots at the same location and restored in the same year	–
	Location	9 groups of plots at the same location	SV
	River km [km]	Distance from the estuary measured along the river course	Both
	Distance to river [m]	Orthogonal distance to the riverbed of the Danube	Both
	Distance to closest biotope [m]	Orthogonal distance to the edge of the closest mapped grassland biotope	Both
	Biotope area [m^2]**	Grassland habitat amount within 500 m radius	–
	MEM1**	Distance-based Moran's Eigenvector Maps variable 1	–
	MEM2***	Distance-based Moran's Eigenvector Maps variable 2	SV
Historical factors	Plot age [yr]	Time since restoration	SV

Variable set	Variable [unit]	Explanation	Model
	$\mathrm{PC1}_{\mathrm{climate}}$	High precipitation during the establishment year followed by dry summer	SV
	$\mathrm{PC2}_{\mathrm{climate}}$	Warm autumn during the establishment year followed by high rainfall in autumn	SV
	$\mathrm{PC3}_{\mathrm{climate}}$	Warm and dry summer during establishment year	SV

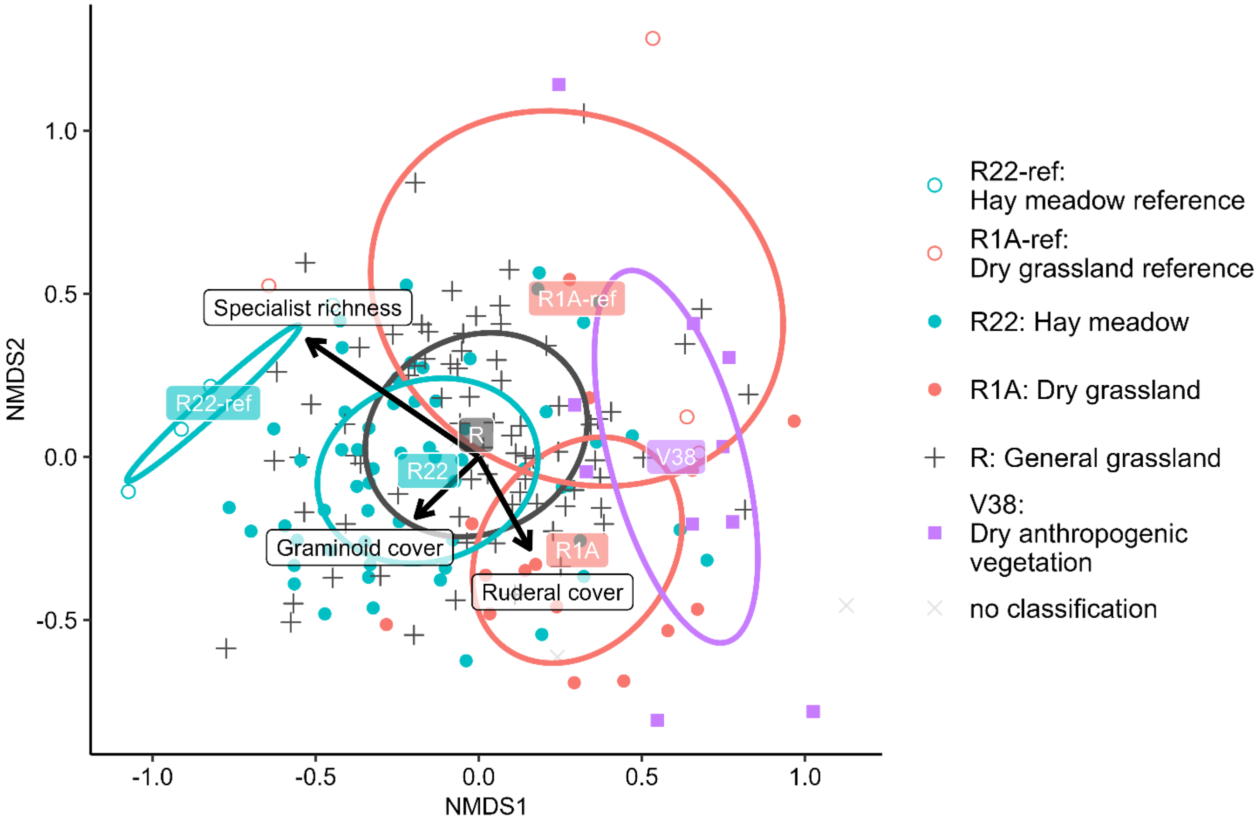
Figures

Figure 1



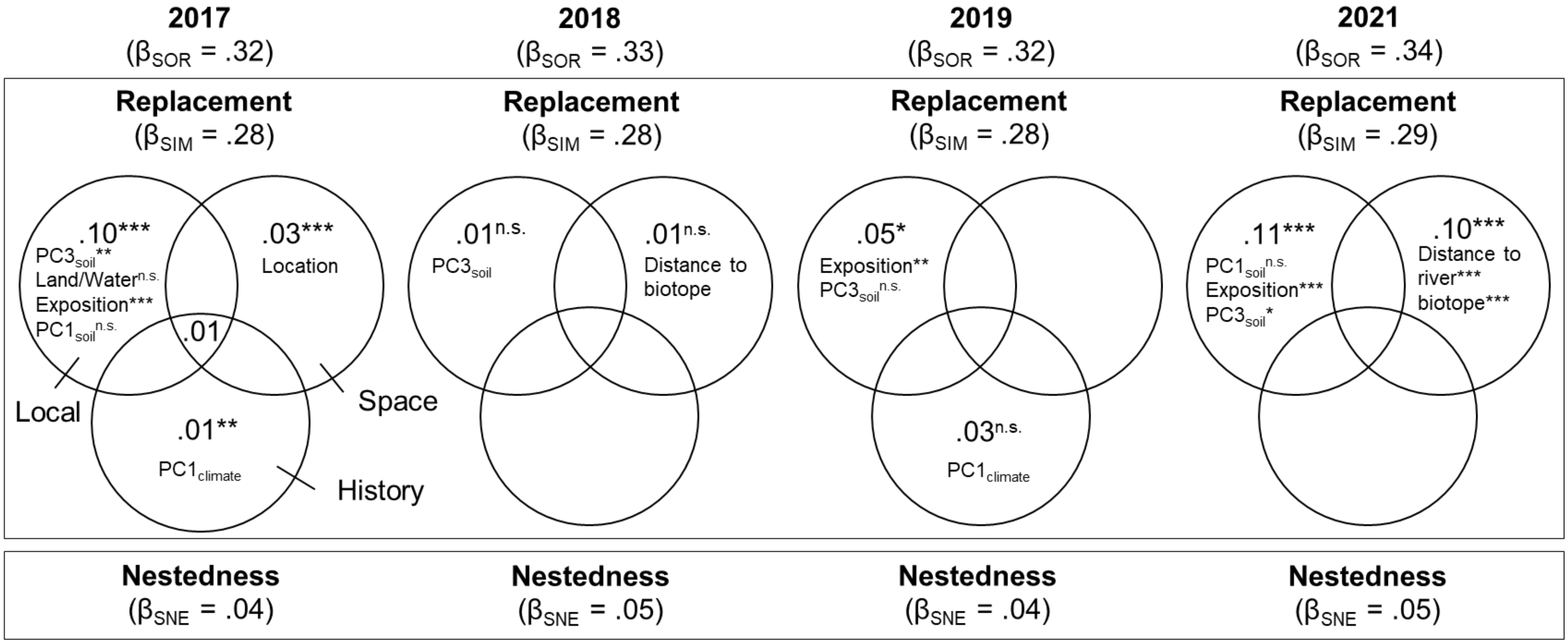
Study sites with dike grasslands on the river Danube in SE Germany. The 41 plots (red dots) were placed on dikes (grey lines) at 12 locations along the river (black line). The labels mark the locations and the restoration year of the site.

Figure 2



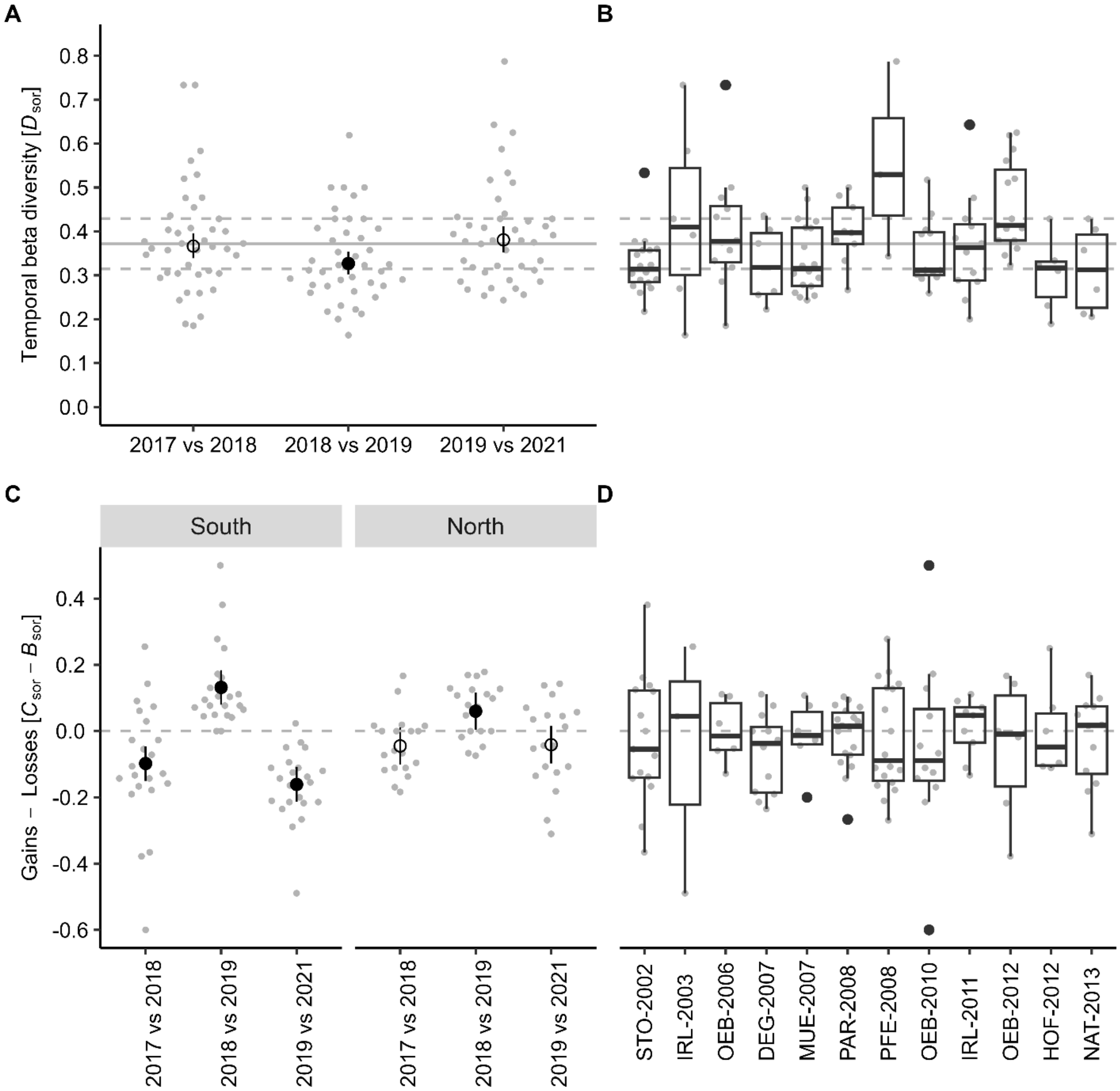
NMDS ordination based on Sørensen dissimilarity of the species compositions of 164 dike plot surveys (filled dots) and eight reference plots (open symbols). The 41 dike plots were surveyed 2017–2021 on the dikes of river Danube, and the reference plots from Bavaria were taken from sPlotOpen (Sabatini et al., 2021). The colors indicate the habitat type of the plot (sensu Chytrý et al., 2020; $R^2 = 0.19$). The vectors indicate the gradients specialist richness vs. ruderal cover ($R^2 = 0.40$; $R^2 = 0.10$) and graminoid cover ($R^2 = 0.07$). 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 of 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 entire set of variables and single variables by partial distance-based redundancy analysis (db-RDA). *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; n.s. = 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.

Figure 4



Year-to-year turnover analyzed by calculating the temporal beta-diversity index (TBI), including 41 plots over 4 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 A8. 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 do not cross the overall mean of the raw data or the 0 line; the locations are sorted by construction year. $R^2_{\mathrm{m}} = 0.28$ and $R^2_{\mathrm{c}} = 0.42$ (A); $R^2_{\mathrm{m}} = 0.41$ and $R^2_{\mathrm{c}} = 0.42$ (C). The boxplots show the median and the box mark the 1st and 3rd quartiles.