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Spatial and temporal homogenisation of freshwater macrofaunal communities in ditches

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Abstract

1. There is a widespread concern that we are witnessing an ongoing homogenisation of ecological communities. However, in contrast to human impacts on spatial patterns in biodiversity, human impacts on the temporal aspects of β-diversity have received little attention. Moreover, the interplay between spatial and temporal β-diversity is poorly understood. To address this knowledge gap, we assessed dissimilarity within freshwater macrofaunal communities of drainage ditches to determine spatiotemporal β-diversity as well as homogenisation in relation to different types of land use.
2. We considered four distinct changes in community composition: spatial turnover, temporal turnover, spatial variation over time, and temporal variation in space, as well as the combined effects of space and time on β-diversity. As a metric of dissimilarity, we calculated the taxonomic Hellinger distance between samples from different locations and time points and correlated these with distance in space and in time, as well as with three spatial variables, including land-use type, and two temporal variables. We studied the effect of interactions between spatial and temporal variables on dissimilarity by applying a permutational analysis of variance.
3. Our results illustrate the importance of changes in community composition in time with respect to temporal turnover, spatial variation over time, and temporal variation in space. While we did not find spatial turnover in community composition, both month and year had a considerable effect. Within a year, β-diversity decreased over the months, yet these assembly patterns differed between years. This suggests major effects of seasonal and year-to-year dynamics on β-diversity. Land use was also observed to be a main driver: ditches in nature conservation areas had higher β-diversity and temporal heterogeneity was lowest in ditches adjacent to the most intensive agricultural land-use category, indicating that agricultural practices can homogenise biodiversity in both space and time.
4. By analysing the spatial and temporal β-diversity patterns in freshwater macrofaunal communities in concert, we have shown that β-diversity is a sensitive and highly informative metric of both spatial and temporal changes in community composition.

KEYWORDS
ditch network, diversity turnover, diversity variation, Hellinger distance, land use

1 | INTRODUCTION

Globally, species richness is declining at a faster rate than ever before (Barnosky et al., 2011; https://www.iucnredlist.org/), but recent studies suggest that at the local scale, species richness is often stable or even increasing (Dornelas et al., 2014; McGill, Dornelas, Gotelli, & Magurran, 2015; Primack et al., 2018). This paradox has raised widespread concern that we are presently witnessing ongoing homogenisation of communities, i.e. a temporal decline of spatial β-diversity (Magurran, 2016; McGill et al., 2015; Primack et al., 2018; Socolar, Gilroy, Kunin, & Edwards, 2016). Emerging evidence confirms this notion (Baiser, Olden, Record, Lockwood, & McKinney, 2012; Gossner et al., 2016; Karp et al., 2012). Given that ongoing homogenisation due to human pressures may decrease ecosystem functioning at higher spatial scales (Mori, Isbell, & Seidl, 2018), it is important to describe and understand the effects of human activities on spatiotemporal changes in communities (Brown, Sokol, Skelton, & Tornwall, 2017; McGill et al., 2015; Mori et al., 2018).

An established framework for examining changes in diversity at larger spatial scales is considering community composition in the context of metacommunities (Leibold et al., 2004). To date, there has been a strong emphasis on *spatial* community heterogeneity or *spatial* β*-diversity* (Logue, Mouquet, Peter, & Hillebrand, 2011). This holds true for scientific studies, but is also particularly prevalent in monitoring efforts to assess the health of aquatic ecosystems in relation to human-induced pressures. In contrast, *temporal* community heterogeneity or *temporal* β*-diversity* is a potentially important dimension that is usually missing, especially in monitoring programmes. However, consideration of temporal β-diversity may be particularly relevant as different subsets of a metacommunity may change at different rates and in a different direction (Campbell, Winterbourn, Cochrane, & McIntosh, 2015), and different human activities may change these rates differently. Therefore, we advocate that changes in spatial and temporal β-diversity are studied in concert. This can be achieved by combining space and time with the two types of β-diversity proposed by Anderson et al. (2011)—turnover and variation—to distinguish four basic types of change in community composition: spatial turnover, temporal turnover, spatial variation over time, and temporal variation in space. While spatial turnover of community composition is relatively well studied (Heino et al., 2015; Socolar et al., 2016), we have little understanding of the importance of temporal turnover and spatiotemporal variation in the composition of natural communities, and to what extent and how these are influenced by human activities (Hawkins, Mykrä, Oksanen, & Vander Laan, 2015, but see Cook, Housley, Back, & King, 2018).

To reduce the knowledge gap on the interplay between spatial and temporal β-diversity, we used a small, well-connected network of drainage ditches to measure the spatiotemporal β-diversity of a freshwater macrofaunal metacommunity. This measurement allowed for studying the joint spatial and temporal components of β-diversity. The ditches are located in the temperate climate zone (Ieromina, Musters, van Bodegom, Peijnenburg, & Vijver, 2016; Ieromina, Peijnenburg, Musters, & Vijver, 2015; Musters et al., in press) and are exposed to different land uses, which creates a mosaic of different abiotic pressures affecting the adjacent aquatic communities. These pressures include the continuous run-off of pesticides and nutrients, which may pose differential selection pressures that can directly (chemical toxicity) or indirectly (resource quality) affect the resident organisms (Allan, 2004; Herzon & Helenius, 2008; Hunting, Vonk, Musters, Kraak, & Vijver, 2016). As such, the study sites allow for assessing the effects of land-use practices on the spatiotemporal composition of these aquatic communities by considering the general null hypothesis that the macrofaunal samples collected in these ditches were derived from a highly connected, spatially and temporally uniform metacommunity, such that the relative species abundances at each location represents a random sample of the relative abundance of the species in the complete metacommunity.

2 | METHODS

2.1 | Research area and data collection

A detailed description of the research area, macrofaunal sampling strategy and taxonomic identification level for each group is given in Ieromina et al. (2015). Briefly, the research area is *c*. 1,600 ha and located in the bulb growing region of The Netherlands (centre: Lat: 52°15′55.66″, Long: 4°28′27.94″). There is an elevation gradient in this lowland area: the height above sea level decreases gradually from a dune nature reserve (the highest site is located 4.26–4.50 m above sea level) towards the polders consisting of bulb-fields and dairy farm grasslands (the lowest site is located 0.49–0.25 m below sea level). The nature reserve area is situated in the north-western part of the polder, so that no contamination arises from the north and north-west side. The flow of ground water is south–west as a result of the natural elevation gradient. For this reason, different agrochemical levels are found at the sites within the research area: lower contamination loadings at the dune locations next to the nature reserve at higher elevation and higher contamination at the sites located at lower elevation downstream (Ieromina et al., 2015). Furthermore, based on a previous study of the quality of organic material from the ditches in the agricultural area for consumption by invertebrates, we know that ditches of the bulb-fields are under stronger human impact than ditches of the dairy farm grasslands (Hunting et al., 2016). So, for this study we divided the ditches into three categories according to the land use in the adjacent fields: dune ditches, bulb ditches, and grassland ditches (Appendix a: Figure S1).

A total of 18 locations in the freshwater ditch system were sampled repeatedly for macrofauna, 14 locations in May, June, July, September, October, and November 2011 and 16 locations in May, July, September, and November 2012, resulting in 148 unique location-time combinations. Three location–time combinations had to be excluded because of insufficient sample quality. We included 10 bulb ditches, four grassland ditches, and four dune ditches. Our samples were not equally distributed over space or time. The spatial distribution was given by the landscape and the temporal distribution by the fact that we restricted the sampling to the growing season. This might bias our results, but we will use the first step of our analysis, viz. the study of the spatial and temporal turnover, to check for possible biases.

Selected ditches were at least 0.7–1 m deep and did not dry up during the year. Water level changes were small and flow was low during our study period. Samples were collected using a dipping net dragged over a total length of 5 m using a multi-habitat sampling strategy (Stowa 2014). Afterwards, all animals were identified to the lowest taxonomic level feasible, the operational taxonomic unit, hereafter called *taxon*. All samples were done by the same researcher, as were the identifications. Dipping nets allow only sampling of macroinvertebrates and small vertebrates, so that some fish (with a maximum length <3 cm, so in the same size class as the macroinvertebrates) were also included in the data set (Ieromina et al., 2015). Appendix b: Table S1 provides an overview of the abundance of all taxa per month.

2.2 | Spatiotemporal β-diversity

For determining β-diversity, a large number of metrics are available (Anderson et al., 2011; Magurran, 2004). In this study, we tested our null hypothesis by using the taxonomic Euclidean distance between the samples per location per date. This metric calculates the dissimilarity between two samples based on the abundance of each taxon. The taxonomic Euclidean distance was in all cases calculated after a Hellinger transformation of the abundance, which takes the square-root of the relative abundance, to avoid the impact of extremely high or low abundances (Figure S2). This means that our metric of dissimilarity is the same as the taxonomic Hellinger distance (Borcard, Gillet, & Legendre, 2011). Other metrices, viz. Bray–Curtis dissimilarity (Bray & Curtis, 1957), Bray–Curtis combined with a Hellinger transformation and the latter applied on biomass instead of abundance of each taxon, were considered but showed remarkably equivalent results (Appendix c: Figure S3–S5 and Table S2–S4).

2.3 | Statistical analyses

The study design considers the general null hypothesis that the macrofaunal samples collected in the ditches were derived from a highly connected, spatially and temporally uniform metacommunity, such that the relative species abundances at each location represents a random sample of the relative abundance of the species in the metacommunity. Deviations from this null hypothesis may be due to dispersal limitations, resulting in increased dissimilarity with increasing distance between samples. Succession may affect community composition, resulting in increased dissimilarity with time. Therefore, we studied the spatial and temporal turnover of the community composition more specifically by testing the following null hypotheses: (1) the dissimilarity in community composition of samples does not increase with distance in space; (2) the dissimilarity in community composition of samples does not increase with distance in time. Likewise, community composition may also be affected by location-specific abiotic factors, such as land use and landscape-wide gradients in soils, and time-specific events, such as weather and seasonality, all resulting in differences in dissimilarity between locations and moments in time. The effects of (interacting) abiotic factors and temporal events on community composition were therefore tested through the following null hypotheses: (1) the median dissimilarity between samples of the same sampling location does not vary with latitude, longitude, or land use of the surrounding fields of the location; (2) the median dissimilarity between samples of the same sampling time does not vary with month or year of the sampling moment; (3) the variance in dissimilarity between samples does not depend on land use, latitude, longitude, year, month, or any of the interactions between these variables.

We first analysed spatial and temporal turnover in community composition as defined by Anderson et al. (2011), i.e. the correlation between taxonomic Hellinger distance and distance in space and time, respectively. We calculated the Euclidean spatial distance between sample locations, as well the Euclidean temporal distance between sample times. In both cases a positive correlation with Hellinger distance is expected, but in order to check for non-linearity we first fitted both linear and loess regression lines using the function *scatterplot()* of the *car* package in R with *span* = 0.75. We tested the correlations with the one-sided Mantel-test of the *vegan* package.

After the initial inspection of spatial and temporal turnover of the community composition, we explored the variation in spatial community composition over time (Anderson et al., 2011) by calculating the median Hellinger distance per month. Variation in temporal community composition in space was explored by calculating median Hellinger distance per ditch. We used medians instead of means for these explorations because we could not assume Hellinger distance to be normally distributed. The median Hellinger distance per month, which is actually a pure measure of spatial β-diversity, was evaluated against time (month and year, both as categorical variables), and median Hellinger distance per ditch, a pure temporal β-diversity, was evaluated against latitude and longitude. To obtain additional insight into the human impacts on temporal β-diversity, we categorised the ditches according to the land use of the surrounding fields: dunes, grasslands, and bulb ditches, respectively. Agricultural fields in our study area have a mean surface area of *c*. 2 ha and are entirely cultivated as either grassland for dairy farming or cropland (bulbs, in this case; Agricola, Hoefs, van Doorn, Smidt, & van Os, 2010). In the dune area, no fields were present and the entire area is managed for nature conservation. In all cases we applied standard statistical testing (ANOVA) using R 3.4.4 (R Development Core Team, 2018).

Because the relationships drawn in this study are based on median dissimilarities and not the complete variance of the Hellinger distance matrix of the complete data set, results of the testing of the significance of the relationships could be misleading. Therefore, and because we additionally wanted to examine the interaction effect of space and time on the variation of community composition, we extended our analyses with a permutational MANOVA (PERMANOVA: function *adonis()* of R package *vegan*), which partitions the variance of the Hellinger distance matrix among the predictor variables land use, latitude, longitude, year, month, and all their possible interactions (Anderson, 2001; McArdle & Anderson, 2001). Land use, year, and month were categorical variables in these analyses. Given that the outcome of this analysis is sensitive to the sequence in which the main terms are added to the PERMANOVA, we also performed the analysis with the two temporal variables (year and month) as first predictor variables.

PERMANOVA is known to be a powerful and robust testing tool for changes in community structure in balanced sampling designs, but it is, like all presently available testing tools, sensitive to heterogeneity in dispersion, i.e. variance or *clustered-ness* within

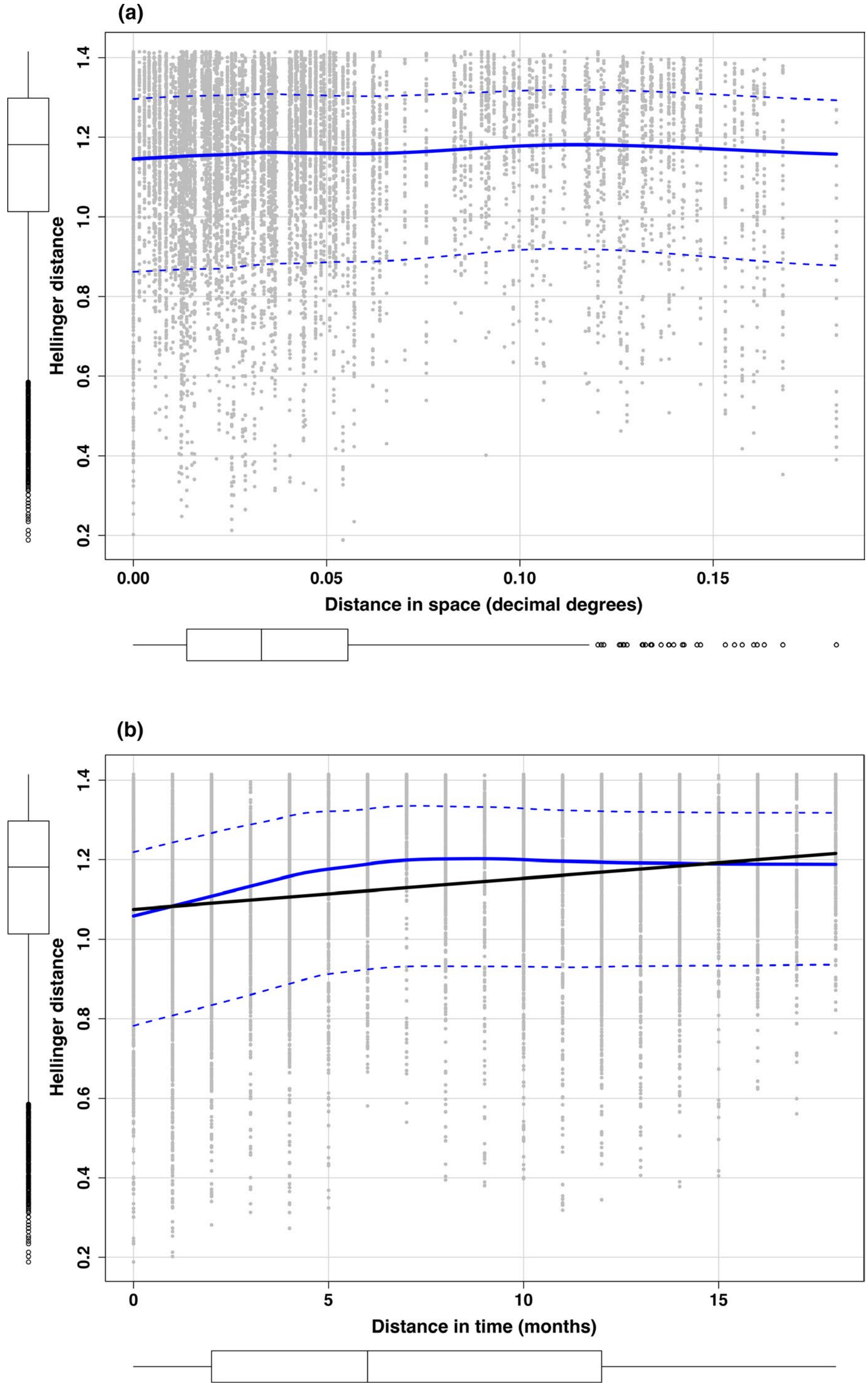

FIGURE 1 The relationship between taxonomic Hellinger distances between aquatic macrofaunal community samples of drainage ditches and (a) distance in space and (b) distance in time (n = 10,440). Blue: loess line; broken lines: one-sided standard deviation from the loess line; black: linear regression line. Box plots along axes: 50% of the observations lie within the boxes; whiskers show 1.5× box range; open dots are outliers [Colour figure can be viewed at wileyonlinelibrary.com]

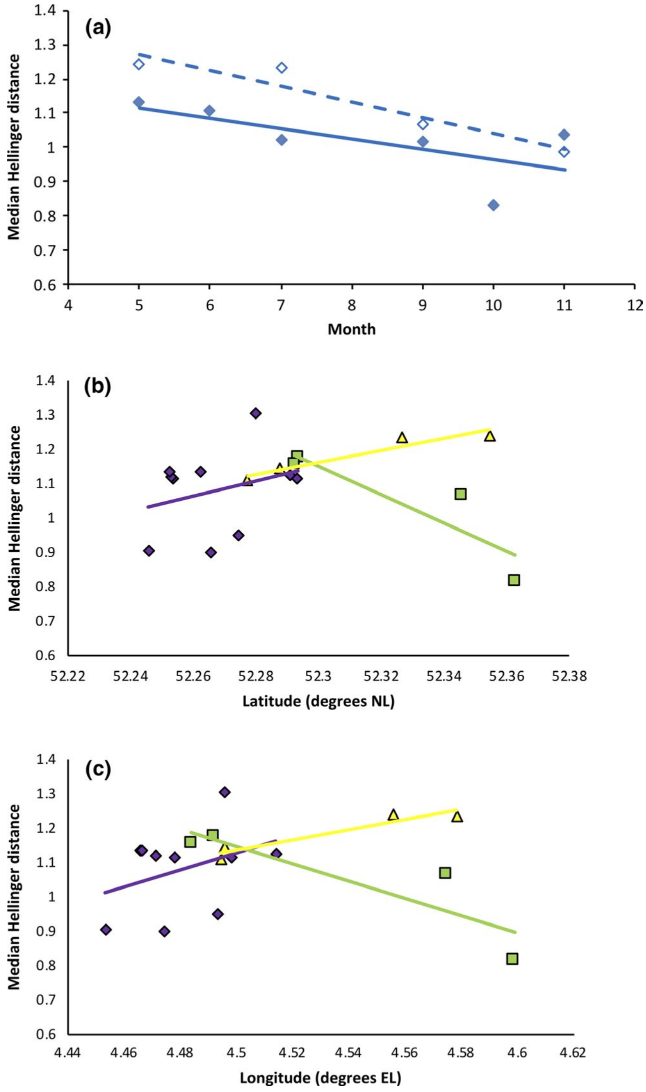

FIGURE 2 Median Hellinger distance between aquatic macrofaunal community samples of drainage ditches (a) per month, (b) per ditch related to latitude of the ditches, and (c) per ditch related to longitude of the ditches. Open symbols: 2012; closed symbols: 2011. Land use: yellow: dune ditches; green: grassland ditches; purple: bulb ditches [Colour figure can be viewed at wileyonlinelibrary.com]

groups, when the design is unbalanced. No technique of controlling for this effect is available yet (Anderson & Walsh, 2013). Our design is unbalanced for land use, year, and month, but we had no a priori reason to expect that the dispersion in Hellinger distance within the groups of these variables is not homogeneous. The homogeneity of dispersion was tested with the function *betadisper()* of R package *vegan* adjusting for bias due to small sample size (Anderson, 2006). The dispersion of Hellinger distance was homogeneous within land-use categories, but varied between years and months (permutation test; *n* permutations = 999; year: *F* = 7.553, *df* = 1; *p* = .012; month: *F* = 9.605, *df* = 5, *p* = .001; land use: *F* = 1.504, *df* = 2, *p* = .245; Figure S6). However, what this means for our testing is as yet impossible to estimate (Houseman, Mittelbach, Reynolds, & Gross, 2008) and as far as we know, no technique for controlling for this potential bias is available yet (Anderson & Walsh, 2013). Therefore, a note of caution on the interpretations of the results of the PERMANOVA is justified.

3 | RESULTS

3.1 | Alpha- versus β-diversity

Since β-diversity may be correlated to α-diversity, we started with evaluating the relationship between α- and β-diversity of the macrofaunal communities of the drainage ditches. The total number of taxa, i.e. γ-diversity, was 170. The number of taxa per sample, i.e. α-diversity, varied between 6 and 32 (mean: 16.6 ± 0.72) and did not show a spatial pattern among sample sites (Pearson *r* = .079, *p* = .343; longitude: Pearson *r* = .085, *p* = .310; latitude × longitude: R^2 = 0.019, *p* = .440; *n* = 145; Figure S7). Neither did the number of taxa per sample show a temporal pattern both between years and months (ANOVA: year: *F* = 0.854, *df* = 1, *p* = .357; month: *F* = 0.915, *df* = 5, *p* = .473; Figure S8a,b). There was an effect of land use. Samples from grassland ditches had a higher number of taxa on average, compared with ditches of other land uses (*F* = 5.924, *df* = 2, *p* = .003; Figure S8c).

Our assumption that the Hellinger distance is not normally distributed was shown to be justified (Figure 1 and Figure S2). There was no correlation between α-diversity and spatial β-diversity when the samples were grouped per month (Pearson *r* = .408; *p* = .242; *n* = 10; Figure S9a), but the negative correlation between α-diversity and temporal β-diversity when the samples were grouped per ditch was marginally significant (Pearson *r* = −.475; *p* = .046; *n* = 18; Figure S9b).

3.2 | Spatial and temporal turnover

Spatial turnover of the community composition was absent: the very weak increase of Hellinger distance over space was not significantly higher than zero (Mantel *r* = .034; *p* = .242; Figure 1a).

However, we found evidence that the temporal turnover of the community composition was present, as illustrated by the Hellinger distance, which showed a significant increase over time (Mantel *r* = .196; *p* = .001; Figure 1b). In other words, the community composition of samples measured shortly after each other is more similar than those measured with a large time period in between. This effect is only present at time distances up to 7 months. Samples measured at time intervals of 7 months and more showed equal dissimilarity.

3.3 | Spatial and temporal variation

The spatial variation in community composition over time, i.e. the median Hellinger distance per month, decreased throughout the year (ANOVA: month: *F* = 11.568, *df* = 1, *p* = .015; year: *F* = 4.921, *df* = 1, *p* = .068; month × year: *F* = 0.528, *df* = 1, *p* = .495; Figure 2a). This indicates that the community composition became less different among ditches within a year. In addition to this short-term temporal effect, we also found a weak effect of year. The year 2012 had

TABLE 1 Results of analysis of variance of the taxonomic Hellinger distances between of all community samples (PERMANOVA)

	df	SumSqs	MSqs	F.model	R^2	*p*-Value
Land use	2	4.840	2.42	4.66	0.051	.001***
Latitude	1	1.186	1.19	2.28	0.012	.009**
Longitude	1	1.000	1.00	1.93	0.010	.023*
Year	1	5.734	5.73	11.04	0.060	.001***
Month	1	4.602	4.60	8.86	0.048	.001***
Land use:Latitude	2	2.782	1.39	2.68	0.029	.001***
Land use:Longitude	2	1.800	0.90	1.73	0.019	.013*
Latitude:Longitude	1	0.487	0.49	0.94	0.005	.492
Land use:Year	2	1.594	0.80	1.54	0.017	.047*
Latitude:Year	1	0.696	0.70	1.34	0.007	.137
Longitude:Year	1	0.317	0.32	0.61	0.003	.925
Land use:Month	2	1.733	0.87	1.67	0.018	.016*
Latitude:Month	1	0.634	0.63	1.22	0.007	.217
Longitude:Month	1	0.669	0.67	1.29	0.007	.182
Year:Month	1	2.408	2.41	4.64	0.025	.001***
Land use:Latitude:Longitude	2	1.047	0.52	1.01	0.011	.444
Land use:Latitude:Year	2	1.431	0.72	1.38	0.015	.066
Latitude:Longitude:Year	1	0.376	0.38	0.72	0.004	.775
Land use:Latitude:Month	2	1.473	0.74	1.42	0.015	.057
Land use:Longitude:Month	2	0.848	0.42	0.82	0.009	.782
Latitude:Longitude:Month	1	0.350	0.35	0.68	0.004	.845
Land use:Year:Month	2	1.262	0.63	1.22	0.013	.181
Latitude:Year:Month	1	0.697	0.70	1.34	0.007	.131
Longitude:Year:Month	1	0.417	0.42	0.80	0.004	.694
Land use:Latitude:Longitude:Month	1	0.475	0.48	0.92	0.005	.520
Land use:Latitude:Year:Month	2	1.216	0.61	1.17	0.013	.202
Latitude:Longitude:Year:Month	1	0.370	0.37	0.71	0.004	.811
Residuals	106	55.031	0.52		0.576	
Total	144	95.472			1	

Abbreviations: a:b, interaction between a and b; *df*, degrees of freedom; *F*.model, pseudo-*F*-ratios; MSqr, mean sum of squares; SumSqr, sum of squares.
p-Values: > .05 * > .01 ** > .001 *** ≤ .001. Testing is based on 999 permutations.

a β-diversity among communities that was higher than 2011 (median Hellinger distance 1.203, resp. 1.101), although this effect was marginally significant.

The temporal variation in community composition in space, i.e. the median Hellinger distance per ditch, showed no correlation with either latitude or longitude. This indicates that the community composition was on average not different at different latitudes or longitudes. Also, median Hellinger distances were not significantly different between land-use types. However, there were significant interactions between land use and latitude (ANOVA: latitude × land use: $F = 3.999$, $df = 2$, $p = .047$), and longitude (ANOVA: longitude × land use: $F = 4.943$, $df = 2$, $p = .027$), thus illustrating that the effect of latitude and longitude on median temporal Hellinger distance of ditches depended on the type of land use (Figure 2b,c).

3.4 | Interactions between space and time

Analysing the combined effect of space and time on the variation in taxonomic Hellinger distance between all samples (PERMANOVA) resulted in an overall R^2 of .424 (Table 1). Thus, 42.4% of the variation in community composition between the samples can be explained by the spatial and temporal predictor variables and their interactions. The combination of spatial variables alone (land use, latitude, longitude, and their interactions) explained 13.8% of the variance, while the combination of temporal variables alone (year, month, and their interaction) explained 13.3%. Interactions between space and time explained the remaining 15.2%. Year explained most of the variance (6.0%, Table 1), followed by land use (5.1%) and month (4.8%). All other main effects and interactions explained <3.0%. Starting with year and month as first predictor variables slightly changed the overall R^2 (41.7% explained), as well as the relative contribution to the variance of the spatial (12.7% explained), temporal (13.8% explained), and space-time interactions variables (15.3% explained), and it lowered the relative importance of land use to the third place, after year and month (Table S5).

Of the two-way interactions, we found significant effects between the spatial variables land use and latitude, respective longitude (PERMANOVA: R^2 =0.029, p = .001, respective R^2 =0.019, p = .013; Table 1; Figure 2b,c) as well as between the temporal variables year and month (PERMANOVA: R^2 =0.025, p = .001; Figure 2a). Moreover, we found significant interaction effects between the spatial variable land use and the temporal variables year (PERMANOVA: R^2 =0.017, p = .047; Figure 3a) and month (PERMANOVA: R^2 =0.018, p = .016; Figure 3b). The higher β-diversity in 2012 compared to 2011 can be ascribed to a higher β-diversity in the dune and grassland ditches, while β-diversity of the bulb ditches was hardly different between the years (Figure 3a). Spatial β-diversity decreased in all land-use categories over the months, but most weakly in the bulb ditches (Figure 3b).

When adding up the explained variance of land use (5.1%) to all the interactions that land use had with other variables, we find that land use is involved in explaining 21.5% of the variance.

4 | DISCUSSION

We observed spatiotemporal patterns in β-diversity of macrofaunal communities in a well-connected network of drainage ditches. These patterns were found for temporal turnover, spatial variation over time, and temporal variation in space. The analysis of the combined effect of spatial and temporal variables on the variation in β-diversity explained additional variation in the composition of the communities, thereby illustrating that the explicit inclusion of both spatial and temporal patterns leads to a greater understanding of ecological communities.

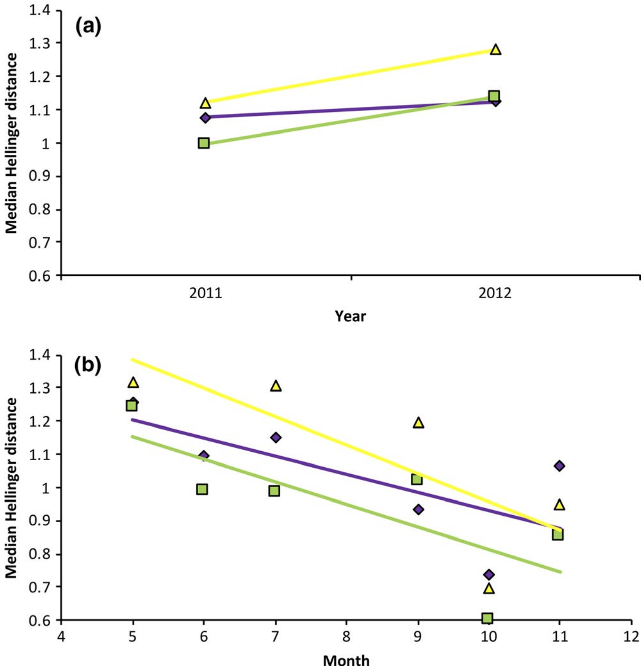

FIGURE 3 Median Hellinger distance between aquatic macrofaunal community samples of drainage ditches (a) per year per land-use type, and (b) per month per land-use type. Land use: yellow: dune ditches; green: grassland ditches; purple: bulb ditches [Colour figure can be viewed at wileyonlinelibrary.com]

Land use proved an important spatial factor explaining the variance in community composition, suggesting that agricultural practices can affect spatial β-diversity as grassland and bulb ditches had lower median β-diversity than the dune ditches. This concurs with other studies showing that spatial β-diversity can decrease with increasing disturbance in a wide array of organisms (Goldenberg Vilar et al., 2014; Johnson & Angeler, 2014; Karp et al., 2012).

The mechanism underpinning the explained variance seems spatial variation rather than spatial turnover in the community composition. Other studies also found that freshwater communities may be only weakly dispersal limited, even up to a distance of 300 km (Cañedo-Argüelles & Rieradevall, 2011; Viana et al. 2015, but see Heino et al., 2015; Downes, Lancaster, Glaister, & Bovill, 2017). A spatial bias due to unequal distribution of our sample location is not to be expected due to the small size and connectedness of our study system where both latitudinal and longitudinal landscape gradients seemed small. This probably excludes spatial turnover as these characteristics in our study system strongly facilitate dispersal of, predominantly, insects (Table S1; De Bie et al., 2012).

By including temporal dynamics in our analysis, we observed that time can explain about the same amount of variance in β-diversity as space and that the explained variance by the interaction between space and time was higher than that by both space and time. We consistently found a significant interaction effect between land use and year and a seasonal decrease in spatial β-diversity for the land-use types considered in this study. The two-way interaction between land use and month showed that a decrease in dissimilarity over the season was present in all land-use types, but significantly weaker in bulb ditches. This strongly suggests that agricultural practices result in a seasonal homogenisation of the adjacent aquatic communities. This is not the result of dispersion of propagules from locations with reproduction to locations without reproduction as this would show similar decreases of spatial diversity. Instead, knowing that community regulation is increased by increasing food limitation (Cadotte & Tucker, 2017; Musters et al., in press), the decreasing dissimilarity is likely to reflect an increase in food limitation or decrease in food quality over time, which is particularly evident in ditches adjacent to bulb fields where a myriad of agricultural chemicals are applied (Hunting et al., 2016, 2017; Vijver et al., 2017).

Quantification of invertebrate diversity at a single time point often occurs in scientific studies, but more importantly are common practice in monitoring efforts to assess the health of ecosystems in relation to environmental perturbations. By considering the temporal aspects of invertebrate community assembly, we observed that more intensive land use may have more profound effects on the temporal dynamics of aquatic communities. A similar pattern was observed by Cook et al. (2018), which was attributed to high concentrations of nutrients enabling generalist species to outcompete seasonal specialists.

It is unlikely that this explains the differences observed in this study, as grassland ditches have higher levels of nutrient than dune ditches (Ieromina et al., 2015), but could potentially be explained by higher levels of pesticides in ditches adjacent to bulb fields (Hunting et al., 2016). Despite this uncertainty, we observed non-linear temporal turnover in community composition (where dissimilarity between samples increased with temporal distance up to 7 months), which indicates a major seasonal turnover in community composition. However, we did not find a clear dip in dissimilarity at the 12 months distance. In other words, seasonality was not so strong that a similar community composition was occurring at the same moment in both years. The inclusion of both month and year in our analyses hints that single time point measurements is unlikely to yield meaningful information on aquatic invertebrate community composition, its dynamic character, and its relation to ecosystem health. Moreover, it stresses the importance of considering within-year seasonal changes separately from between-year changes to prevent bias due to unequal distribution in time of sampling, and shows how time specific sampling can be employed to reliably compare invertebrate community diversity at different locations that have inherently different dynamics in community assembly processes.

5 | CONCLUSIONS

While spatial patterns in biological organisation and human impacts on spatial β-diversity have received a lot of scientific attention, the temporal component of β-diversity and how this metric is affected by human activities has been largely ignored. By analysing the spatial and temporal β-diversity patterns in freshwater macrofaunal communities in concert, we show that β-diversity is a sensitive and highly informative metric of community changes in both space and time. Variance in β-diversity was better explained by predictor variables than variance in α-diversity (Ieromina et al., 2015), most variance in β-diversity was explained by land use and its interactions with other variables. Beta-diversity might therefore serve as a more sensitive metric of human impacts than α-diversity in a wide range of ecosystems (e.g. grasslands: Gossner et al., 2016). This reinforces the suggestion that disturbances may particularly affect β-diversity, and that agricultural practices may reduce the temporal dynamics of communities, thereby homogenising biodiversity in both space and time.

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AUTHOR CONTRIBUTIONS

C.J.M. designed the study, did the statistical modelling and analyses, and wrote the draft paper; O.I. did field sampling, taxonomic identification and constructed the datasets; O.I. and H.B. structured the data; E.H., M.S., E.C., M.V., and P.v.B. contributed to the study design and the conceptual improvement of the manuscript; all authors substantially revised the subsequent drafts.

DATA AVAILABILITY STATEMENT

Our data are available on https://datadryad.org/; https://doi.org/10.5061/dryad.5q5b554

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SUPPORTING INFORMATION

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

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