Statement of authorship

DH, HH, SH, EB, EL and ES conceptualized the study, DH performed statistical analyses and wrote the manuscript, all other authors contributed data and substantially contributed to revisions of the draft.

Title: The spatial ~~distribution of species composition~~ heterogeneity in species composition constrains plant community responses to herbivory and fertilization

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Running title: Beta-diversity constrains temporal turnover

Type of article: Letter

Word counts: Abstract 151, Main text 4041

Number of references: 66

Number of Figures: 4, Tables: 0, Text boxes: 0

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Abstract

Changing environmental conditions result in substantial shifts in the composition of communities. The associated immigration and extinction events are likely constrained by the spatial distribution of species. Still, most studies on environmental change quantify the biotic responses at single spatial (time series within a single plot) or temporal (spatial beta-diversity at single time points) scales, ignoring their potential interdependence. Here, we use data from a global network of grassland experiments to determine the dependence of temporal community turnover (separated into changes in species richness and species replacement) on species pool size and spatial compositional differences across plots, and examine the influence of fertilization and herbivore exclusion on these relationships. Sites with more spatially heterogeneous communities showed significantly higher rates of annual turnover in control and treatment plots independent of species pool size. Integrating spatial aspects of biodiversity will improve our understanding of consequences of global and anthropogenic change on community dynamics.

Keywords

Beta-diversity, diversity, fertilization, grassland, nitrogen, Nutrient Network (NutNet), spatial heterogeneity, species composition, temporal turnover

Introduction

Global warming, increased nutrient input, and habitat fragmentation require species to either adapt, disperse or go extinct. The consequences are major shifts in species composition (Walther *et al.* 2002; Feeley *et al.* 2011; Moritz & Agudo 2013), high rates of temporal species turnover (Hillebrand *et al.* 2010; Larson *et al.* 2016), biological invasions (Seabloom *et al.* 2013, 2015) and species loss (Brook *et al.* 2008; Pimm *et al.* 2014). Depending on the balance of the resulting colonizations and extinctions, these compositional changes may or may not result in changes in overall species numbers (Hillebrand *et al.* 2010, Dornelas *et al.* 2014; Elahi *et al.* 2015). Understanding species temporal turnover and identifying its drivers and dependencies will therefore help to interpret the substantial differences in compositional changes across communities in response to similar environmental alterations (Jackson & Sax 2009; Avolio *et al.* 2015; Hillebrand *et al.* 2017) and ultimately provide more reliable predictions of the functional consequences of environmental changes (Fox & Kerr 2012).

Ongoing species changes have theoretical underpinnings that can guide our expectations, but need effective tests to determine their relevance for predicting turnover in response to global change. Temporal turnover can reflect changes in the relative abundance of persisting species as well as immigration and local extinction of species (Smith *et al.* 2009). Whereas changes in relative abundances reflect internal shifts in dominance, immigration and replacement of species involve changes in species identity and require the presence of additional species in the regional species pool. Large species pools can be the result of heterogeneous environmental conditions in space and time. These provide highly variable niche space and are therefore likely to promote the coexistence of higher numbers of species as well as more distinct local communities (Questad & Foster 2008; Stein *et al.* 2014). In addition, high degrees of specialization of local communities in heterogeneous landscapes and mechanisms such as dispersal limitation (Pinto & MacDougall 2010) can result in potentially higher turnover rates under changing environmental conditions. Thus, temporal shifts in species composition in general and in response to environmental changes are intrinsically related to spatial beta-diversity, as described in concepts such as the species-time-area-relationship (STAR) (Adler *et al.* 2005; Korhonen *et al.* 2010;

Stegen *et al.* 2013). Here, we refer to compositional changes over time as ‘temporal turnover’ whereas we use the term ‘beta-diversity’ only to denote compositional differences of communities in space.

Despite the acknowledgement that temporal shifts in composition should be understood in a spatial context, it is common practice in global change experiments to analyze data from single plots independently from their surroundings. The primary data feeding into synthesis studies on biodiversity change in response to global change drivers such as fertilization, consumer loss, or warming (Walker & Wahren 2006; Hillebrand *et al.* 2007; Murphy & Romanuk 2014) mainly consist of diversity estimates at the plot scale, treating replicate plots as independent units sampled from a homogeneous landscape. This approach ignores possible effects of the regional species pool on the changes in species composition in response to treatment application or at least assumes that these effects are negligible compared to treatment effects (Seabloom *et al.* 2015; Harpole *et al.* 2016). Compositional change in response to changing environmental conditions might be limited if low spatial heterogeneity in community composition reduces rates of immigration and consequently constrains temporal turnover. Thus, differences in the magnitude of the biodiversity response between studies, systems, or organism groups might not only reflect differing impacts of drivers, but also varying abilities to respond due to the spatial species distribution of the surroundings (Collins *et al.* 2018). This makes direct comparison of compositional responses to environmental change difficult.

In addition, many common turnover measures share two inconvenient properties: the sensitivity to overall species richness (Rice & Belland 1982) and the inability to distinguish between community turnover caused by changes in species number as opposed to replacement of species (Baselga 2007). Both turnover components contribute to overall turnover measures, but can result from rather different phenomena. While changes in species richness might reflect non-random processes of species loss caused by altered environmental conditions, species replacement can be the consequence of mechanisms such as environmental sorting or successional gradients.

Here, we apply a structural equation model to data from a globally replicated nutrient addition and herbivore exclusion experiment. We use a recently introduced approach to separate overall community changes into turnover reflecting changes in species numbers and turnover reflecting species replacement (Baselga 2010) and test the following three core hypotheses: (1) Increased spatial heterogeneity in species composition increases the rate of temporal turnover of communities in response to manipulated resource and consumer conditions. (2) The spatial heterogeneity of species composition~~(beta-diversity)~~ responds to site-specific environmental conditions such as spatial and temporal environmental variability. Using marginal generalized linear~~a linear mixed~~ models, we further test the hypothesis that (3) directional shifts in community composition in response to an experimentally altered resource and consumer environment increase with increasing site-level beta-diversity. Our analyses reveal that the initial spatial community heterogeneity ~~distribution of species~~ strongly affects the strength of community responses to changing environmental conditions.

Material and Methods

The data used in this study were collected as part of the Nutrient Network (NutNet), a globally distributed replicated grassland experiment. Manipulations include nutrient supply via addition of nitrogen (N), phosphorus (P), and potassium and micronutrients (K+), and the exclusion of vertebrate herbivores via fencing (see Borer *et al.* 2014*a* for more details). All treatments were applied to 5x5 m plots using a completely randomized block design. Each site consists of at least 3 (maximum 6) blocks of 10 plots each. For our analyses, we included data from all sites with measurements from at least four years (one pre-treatment year plus three to five years of treatment application) which amounted to 41 sites (131 experimental blocks). In our analysis we focused on temporal turnover in treatment plots that allow us~~ed~~ to test for effects of addition of all major nutrients and herbivore exclusion, i.e. untreated controls (Ctrl), plots fertilized with all three major nutrients (NPK), plots without grazers (fence), and plots treated with both nutrient addition and grazer exclusion (NPK+fence).

Sampling and laboratory analyses of all plots and samples follow the same protocol allowing direct comparison of data from all sites. Plant community composition and soil chemistry were measured at the plot level in the year prior to treatment application (Y0), and composition was subsequently measured annually at peak biomass. Community composition was determined by independently estimating the areal cover of each species to the nearest 1%. Species taxonomy was reconciled across sites and through time within a site to minimize artificial “turnover” due to nomenclature changes through time (Lind 2016). Soil samples were collected at 0 – 10 cm depth. Here we used the following soil chemistry parameters: C, N, P, K, Ca, Mg, S, Na, Zn, Mn, Fe, Cu, B and pH (Borer *et al.* 2014a). Additionally, geographical parameters (latitude, longitude, elevation) and ambient light were recorded for each site.

All statistical analyses were performed in R statistical computing (R Core Team 2016). For this study, we were interested in how species turnover in a plot over time (temporal turnover) is affected by the initial species pool size and spatial distribution of species across all plots within one block, i.e. block richness and within-block beta-diversity before treatment application (Y0). We calculated block richness as the total number of plant species present in a block and within-block beta-diversity as the Jaccard's Dissimilarity Index (Jaccard 1912) across the ten plots in each block (‘simba’ package, Jurasinski & Retzer 2012). Temporal turnover was represented by~~calculated as~~ the averaged presence-absence based Jaccard dissimilarity between subsequent years (Y0-Y1, Y1-Y2, Y2-Y3). We ~~deliberately~~ applied a presence/absence based measure of dissimilarity and turnover here, as our focus lies on species replacements which are constrained by the regional species pool, assigning equal weight to rare and common species (Anderson *et al.* 2011). We additionally separate overall temporal species turnover into two components capturing different aspects of community change. The first~~a~~ component represents changes in species composition resulting from species replacement (”turnover”) whereas~~and~~ the second~~a~~ component represents community richness changes caused by an imbalance between immigration and loss of species (”nestedness”) (Baselga 2010; Baselga & Orme 2012)~~, which will alter richness over time (Baselga 2010; Baselga & Orme 2012)~~. Differences in the magnitude of these two components across experimental units, can reflect differing drivers or mechanisms governing compositional changes in communities (Baselga 2010). The partitioning approach is described in Baselga (2010) and was calculated using the ‘betapart’ package (Baselga & Orme 2012). To facilitate interpretation of the two components in our temporal context we deviated from~~altered~~ the terminology used by Baselga (2010) and refer to the “turnover” component as compositional changes due to species replacement (TTO_{rep}) whereas “nestedness” will be referred to as changes in species richness (TTO_{rich}):

TTO_{Jac} = TTO_{rep} + TTO_{rich}~~ = (b+c)/(a+b+c)~~ = 2*min(b,c)/(2*min(b,c) + a) + ((max(b,c) – min(b,c))/(a + b + c))*(a/(2*min(b,c) + a)),

where overall temporal turnover TTO_{Jac} ('Jaccard') is expressed as the sum of TTO_{rep} ('replacement') and TTO_{rich} ('richness'). Here, *a* represents the number of species present in both years, *b* and *c* represent the numbers of species present in only one of the two years. For more details on the mathematical derivation of the above equation see Baselga (2010). Values can range from 0 and 1. Zero temporal turnover indicates no change in community composition. A TTO_{rep} of 1 indicates the complete replacement of all species in the community whereas a TTO_{rich} value of 1 would indicate extinction or immigration of all species in the community.

For the estimation of spatial *environmental* variability we calculated Euclidean distances (‘vegan’ package, Oksanen et al. 2016) for standardized soil parameters (nutrients and pH) and ambient light measurements across all plots of each block prior to initiation of treatments. To describe long-term temporal environmental variability, we standardized and aggregated variability of site level mean annual precipitation and temperature to obtain a single measure representing climatic conditions. The data were obtained from Bioclim, which is part of a set of publicly available global climate layers at 1km resolution (Worldclim, http://worldclim.org/bioclim).

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~~For the quantification of possible dependencies of environmental variability and species diversity and their effects on the two temporal species turnover components~~To test our hypotheses using the specific measures described, we ~~set up~~developed an initial~~ a~~ structural equation model~~ (SEM)~~. To test our first hypothesis that spatial heterogeneity in species composition promotes higher rates of temporal species turnover we included~~mplemented~~ pathways from block beta-diversity to the two turnover components. Additionally, we allowed for direct effects of block richness on both aspects of temporal turnover (Allan *et al.* 2011) to account for effects of species pool size. For our second hypothesis that environmental variability in space and/or time is a driver of pre-treatment richness and beta-diversity, we incorporated pathways from the temporal (climate) and spatial (soil conditions and light) environmental variability measures to block richness and beta-diversity. We also included direct links between the environmental variability measures and temporal species turnover. As stated in the literature on species area relationships (Connor and McCoy 1979) and species-time-area-relationships (Adler *et al.* 2005), species richness and spatial beta-diversity are likely to be correlated, which also applies to our dataset. We therefore included~~added~~ a direct pathway from block richness to block beta-diversity. Alternative model formulations and model output can be found in the supplementary material (Appendix S1.1.3).

All analyses were performed~~run~~ using robust estimation procedures implemented in the 'lavaan' (Rosseel 2012) and 'lavaan.survey' (Oberski 2014) packages accounting for non-normality in some of the variables and the nested structure of the data (plots within blocks within sites). We ran separate SEM analyses for each treatment and the control plots and subsequently compared estimates of the respective pathways. Soil and environmental variables were not available for all sites reducing our sample size (Ctrl: 96, NPK: 95, fence: 79, NPK+fence: 80). Model fit was assessed based on several fit measures available as part of the model output in the 'lavaan' package (Appendix S1.1.2).

To test our third hypothesis that beta-diversity not only constrains annual turnover but also directional shifts in community composition in response to treatment application, we compared the community composition at the beginning of the study with the composition in the same plot after one to five years of treatment application. We again separated overall temporal turnover (Jaccard dissimilarity) into both turnover components (TTO_{rep}, TTO_{rich}) and tested for differences between the control and treatment plots. ~~In order to account for the nested structure of the data we applied linear mixed effects models (LMM) with nested random effects accounting for dependencies of measurements from the same plot, block and site ('lme4' package, Bates *et al.* 2015). Statistical significance was determined by bootstrapped confidence intervals for all model estimates ('boot' package, (Davison & Hinkley 1997; Canty & Ripley 2017)). Marginal and conditional R^2 served as measure of explained variance ('MuMIn' package, Barton 2016).~~ We fit marginal generalized linear models using the generalized estimating equations (GEE) approach from the ‘geepack’ package (ref.) to account for the nested structure of the data.

Results

Overall, mean annual turnover varied considerably across sites ranging between 0.12 and 0.86 (Appendix S1.1.1). After four years of treatment application, compositional dissimilarity to control ranged from 0 to 1 (from none to complete turnover) indicating a substantial change in species composition at some sites (Appendix S1.1.1).

The SEM analysis yielded a significant coefficient for the path from beta-diversity to the temporal turnover component reflecting species replacement (TTO_{rep}), with consistently positive effects across all treatments and the control (Fig.1). Thus, temporal turnover by species replacement was higher when the species composition in the surrounding area was more heterogeneous. The model further revealed that plots within high richness blocks experienced less mean annual turnover in the form of TTO_{rep} than plots in blocks with low species richness. Within grazer exclusion treatments (Fence and NPK+fence), block richness was negatively associated with changes in species richness due to extinction and/or immigration (TTO_{rich}). The path coefficient between block richness and beta-diversity confirmed the expected positive association between these two variables. With regard to influences of environmental variability on species diversity, the model revealed a positive effect of mean annual climate (temperature and precipitation) variability on beta-diversity, which was consistent across treatments. We also found a negative effect of climate variability on richness as well as significantly positive effects of spatial environmental variability on beta-diversity, but only in the control and the nutrient addition plots. It should be noted that the differences in pathway significance describing effects of environmental variability on richness and beta-diversity across treatments arise, in part, from the use of different data subsets. A number of high diversity sites did not apply herbivore exclusion treatments resulting in smaller sample sizes and shorter diversity gradients in the data sets including fences (Appendix S1.1.4).

Overall model fit (Satorra-Bentler scaled Chi-square tests accounting for non-normality in the data) measured as the deviation of the variance-covariance matrix predicted by the model from the variance-covariance matrix of the observed variables resulted in p-values ranging from 0.30 (NPK) to 0.77 (Fence). Non-significant p-values indicate no detectable differences between the observed and predicted data, i.e. congruence of model and observations. Model fit was confirmed by further fit indices, RMSEA and residuals of the modeled and measured covariance matrices (Appendix S1.1.2). For completeness, we ran SEM analyses using abundance-based turnover metrics (Appendix S1.1.4). Their results corroborated the general relationships found in our presence-absence based turnover analysis.

Mean annual turnover rates showed considerable variation across sites, but relatively little difference in the association between beta-diversity and annual turnover across control and the three treatments (Fig. 2). Similarly, the linear model~~LMM~~ analysis on directional composition changes over up to five years revealed increasingly differing community compositions in all treatments as well as the controls (Fig. 3), and confirmed the significant effect of initial beta-diversity (0.357 +/- 0.106, p-value <0.001~~0.288, CI: 0.132, 0.443~~) on overall turnover independent of the type of treatment (Appendix S1.2). However, the slope of increasing composition changes (TTO_{Jac}) was significantly stronger in the combined nutrient addition plus grazer exclusion treatment (NPK+fence) than in the control plots (0.018 +/- 0.006, p-value = 0.002~~0.020, CI: 0.009, 0.031~~; see Appendix S1.2.1 for complete LMM results). We further found that whereas richness changes in the control plots stayed at a similar level throughout the duration of the study, ~~the NPK (0.023, CI: 0.013, 0.033) and NPK+fence (0.025, CI: 0.014, 0.036) treatments~~all the treated plots showed increasingly higher levels of composition change due to either species loss or immigration (~~Fig. 3~~NPK: 0.022 +/- 0.007, p-value = 0.001; fence: 0.011 +/- 0.005, p-value = 0.46; NPK+fance: 0.025 +/- 0.008, p-value = 0.001). These higher levels of compositional alterations in form of richness change were driven by higher rates of species extinction in the fertilized plots as opposed to relatively constant numbers of immigrations over time and across treatments and control (see Appendix S.1.2.2). Compositional differences in the form of species replacement increased in all treatments and the control, but the increase was significantly less pronounced in the NPK treatment compared to the controls (~~-0.019, CI: -0.033, -0.005~~0.019 +/- 0.008, p-value = 0.015). ~~Overall, most of the variation was~~

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~~explained by across site differences. The fixed effects beta-diversity and treatment captured only little of the total variation in the turnover measures (TTO~~~~$_{rep}$~~~~: 4%, TTO~~~~$_{rich}$~~~~: 3%, TTO~~~~$_{Jac}$~~~~: 10%), whereas conditional R~~~~^{2}~~~~ values (fixed and random effects) indicated much higher levels of explained variance (TTO~~~~$_{rep}$~~~~: 50%, TTO~~~~$_{rich}$~~~~: 31%, TTO~~~~$_{Jac}$~~~~: 64%).~~

Discussion

Our analysis of temporal turnover patterns shows that the rates of ~~species~~ compositional turnover~~exchange~~ among years are higher in sites with higher beta-diversity. Additionally, fertilization and the combined fertilization plus fencing treatment led to a greater number of extinctions (increase of TTO$_{rich}$ with duration of treatment application) whereas fencing on its own resulted in similar rates of colonization or extinction as in the control plots.

A comparison of our results with the analysis of species richness changes in the same experiment (Borer *et al.* 2014b) adds further details to understanding the differences in community changes across treatments. Borer et al. (2014b) show that in the majority of sites species richness declined with fertilization alone, whereas the effects of fencing and fencing plus nutrient addition did not consistently affect richness. The latter was attributed to the effect of vertebrate consumers on light availability: richness increased with grazing if grazing enhanced light availability, but richness declined when removing grazers reduced ground-level light (Borer *et al.* 2014b). We show that the annual compositional shifts induced by fencing, fertilization or both were very similar in magnitude (Fig. 3 left panel) and rather driven by beta-diversity or site-specific conditions. Yet, compositional changes after five years of treatment differed in the magnitude of the temporal turnover components. Fertilization by itself led to increasingly negative changes in species richness, but to a decrease of species turnover in form of species replacement (Fig. 4). In contrast, grazer exclusion resulted in values very similar to both turnover components in the control plots. Interestingly and analogous to the findings in Borer et al. (2014b), grazer exclusion seemed to offset the negative effect of fertilization on species replacement in the combined NPK+fence treatment, which showed higher values of TTO$_{rich}$ and TTO$_{rep}$, resulting in the observed higher overall turnover. In terms of the ecological consequences of fertilization, our results indicate that irrespective of whether species loss is caused by a reduction in niche dimensionality (Harpole & Tilman 2007) or shading effects due to increased biomass production (Hautier *et al.* 2009), higher levels of beta-diversity and larger species pools are likely to buffer fertilization effects on community composition by mediating species loss and allowing for higher turnover.

Beta-diversity enhanced species turnover rates and was positively correlated with the number of species in a block. Higher levels of block species richness, however, led to consistently lower exchange of species identities (TTO_{rep}) in all treatments. These negative correlations between richness and temporal turnover (White 2004; Shurin 2007) can result from mechanisms including limited success of colonization or species coexistence patterns in response to environmental variability and have been frequently reported and discussed in the literature (Shurin 2007; Matthews & Pomati 2012; Pandit & Kolasa 2012). Our model further indicates that climatic (temporal) and soil nutrient (spatial) heterogeneity result in higher beta-diversity which is consistent with ecological niche theory (Hutchinson 1961) and corroborates findings from studies spanning a wide range of ecosystems and organism types (Veech & Crist 2007; Questad & Foster 2008; García-Palacios *et al.* 2012; Heino *et al.* 2013). The negative association of climate variability and species richness could be ascribed to latitudinal richness patterns (Hillebrand 2004) as species diversity tends to be higher in lower latitudes where deviations from annual temperature and precipitation means are less pronounced.

In the mixed effects analyses on compositional changes over 1 to 5 years of treatment application strikingly little variance of the turnover components was explained by the fixed effects (treatment and beta-diversity). Site-specific factors accounted for a much larger amount of variation in the data. Hence, beta-diversity seems to be one aspect constraining composition changes and investigation of site-specific conditions will be necessary to gain a more comprehensive picture of what is driving community change in general and as a consequence of environmental change.

Our results highlight the value of integrating~~need to integrate~~ spatial and temporal aspects of turnover in analyses of community change over time, two factors that are often considered separately although their interactive effects on turnover have been demonstrated before (Adler *et al.* 2005). Most analyses of temporal turnover in a macro-ecological context have been conducted using a within-plot perspective (Korhonen *et al.* 2010; Shade *et al.* 2013), i.e. ignoring effects from outside of the experimental units. Likewise, most analyses of biodiversity change with environmental drivers have interpreted differences in the response of richness, evenness or other diversity metrics as an emergent property of the local community, not of the regional heterogeneity in diversity (Hillebrand *et al.* 2007; Murphy & Romanuk 2014). Here we show that annual turnover and treatment-induced dissimilarity (0-100% compositional turnover already after four years of treatment application) vary substantially across sites, which classically is interpreted as different sensitivities to the environmental driver. However, our analyses clearly demonstrate that changes in species composition, measured as annual species turnover and dissimilarity in composition after treatment application, both significantly increase with increasing levels of beta-diversity, which is in turn affected by the species pool. Thus, the variation in turnover and treatment-induced dissimilarity is caused by the sites differing in their response potential, as only sites with high beta-diversity provide the scope for additional species colonizing the local patch when conditions change. In other words, adaptation of species composition to altered environmental conditions not only depends on the strength of these alterations and the number or identity of species locally present, but is constrained by how heterogeneously these species are distributed in space (beta-diversity). These results have fundamental consequences for the analysis of compositional shifts in observational time series and in experiments that are open to colonization: without explicitly considering the spatial context, which determines the size of the species pool that is available for immigration, a given shift in composition (and species richness) cannot be interpreted or compared between sites. Community A might respond more to a certain driver than community B because the species in A are more sensitive to this driver, or because community A is embedded in a region with additional species being present and capable of immigration (see also (Hautier *et al.* 2018).

Our analysis shows that without the distinction of turnover due to richness changes as opposed to species replacement, impacts of altered environmental conditions might be missed, because baseline overall turnover is an inherent property of most ecological systems (Hillebrand *et al.* 2017) and can equal overall turnover despite significant changes in both turnover components (Fig. 4). In addition, the large proportion of the Jaccard dissimilarity explained by species replacement demonstrates that a focus on species numbers only can be a very coarse measure of biodiversity change, potentially masking substantial changes in species identity and functional traits (Hillebrand *et al.* 2010, 2017; Dornelas *et al.* 2014; Jones *et al.* 2017). In this regard, our results further suggest that factors constraining turnover, such as homogenization of environmental conditions or plot-level species richness, may also change ecosystem stability. If temporal turnover in composition is a (or even the) mechanism allowing for functional stability under changing conditions (Allan *et al.* 2011; Loreau & de Mazancourt 2013; Mazancourt *et al.* 2013; Hautier *et al.* 2014), then any limitation of turnover will affect local and regional stability (Wang & Loreau 2016; Wilcox *et al.* 2017).

We provide clear evidence that spatial beta-diversity at the onset of an experiment constrains the ability of a local assemblage to alter its composition over time and in response to changes in environmental conditions. Variation in response magnitudes thus may not reflect the actual impact of a change on composition, but the scope for compositional change due to the presence of additional species in the region.

Acknowledgements

DH and HH acknowledge funding by the Ministry of Science and Culture, State of Lower Saxony, through the project BEFmate. This work was generated using data from the Nutrient Network (http://www.nutnet.org) experiment, funded at the site-scale by individual researchers. Coordination and data management have been supported by funding to E. Borer and E. Seabloom from the National Science Foundation Research Coordination Network (NSF-DEB-1042132) and Long Term Ecological Research (NSF-DEB-1234162 to Cedar Creek LTER) programs, and the Institute on the Environment (DG-0001-13). We also thank the Minnesota Supercomputer Institute for hosting project data and the Institute on the Environment for hosting Network meetings.

Field Code Changed

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Figures

Figure 1

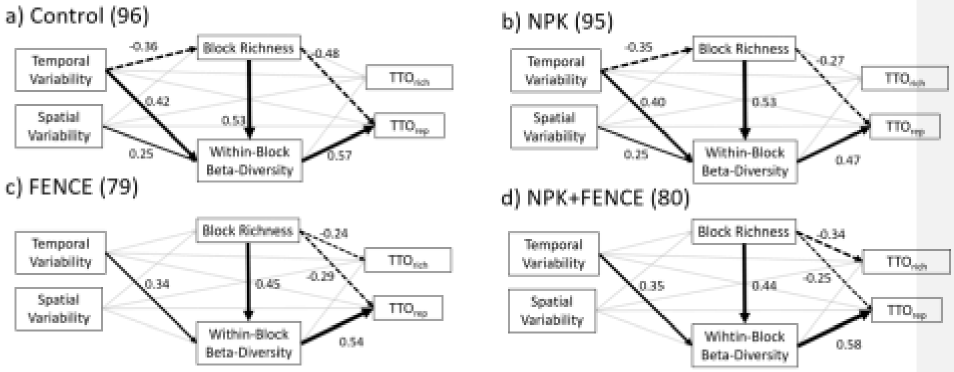
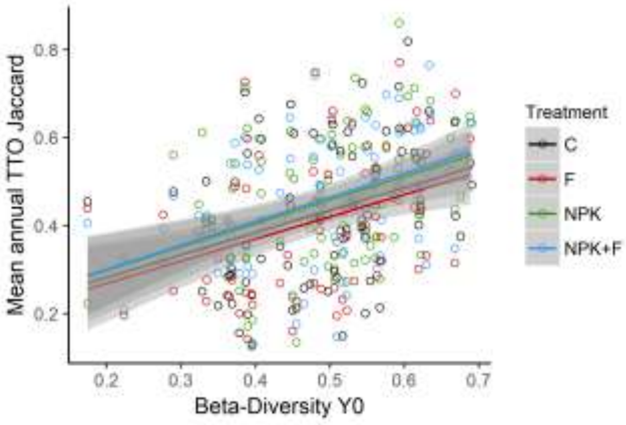


Figure 2



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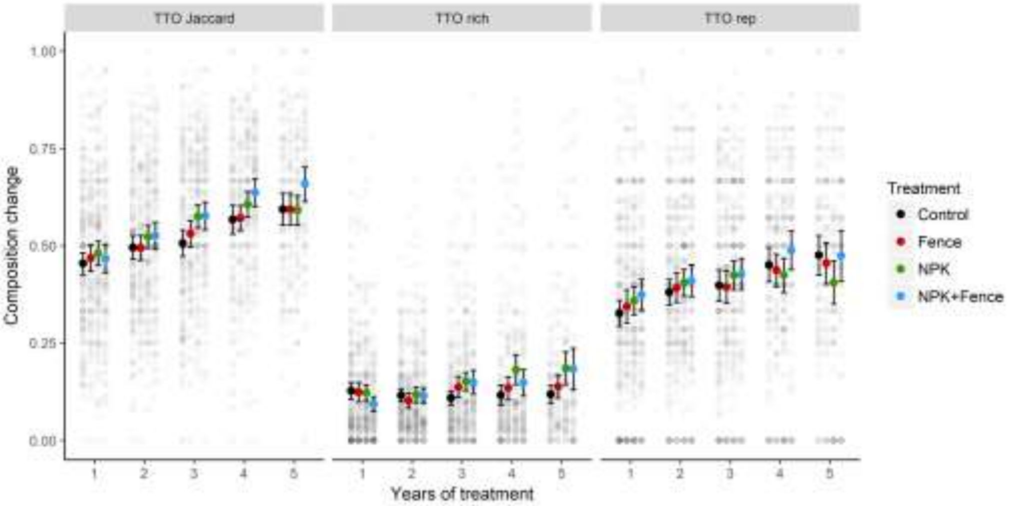

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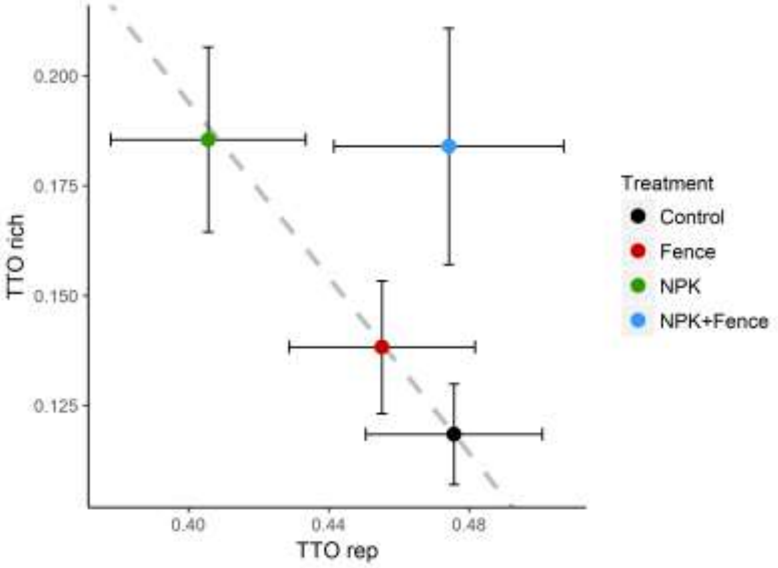

Figure legends

Fig.1: Structural equation model path diagram including all significant pathways in black and non-significant pathways in gray for a) control plots, b) nutrient addition treatment (NPK), c) grazer exclusion treatment (F) and d) combined nutrient addition and grazer exclusion treatment (NPK+F). The displayed estimates are standardized path coefficients. For a detailed statistical output on model fit see Appendix S1.1.2. The width of the arrows reflect the strength of the according pathway. Line type represents positive (solid) and negative (dashed) path coefficients.

Fig.2: Relationship between block beta-diversity prior to treatment application and mean annual turnover rates. The colors indicate data from control (C, black) and the three treatments grazer exclusion (F, red), nutrient addition (NPK, green) and nutrient addition plus grazer exclusion (NPK+F, blue).

Fig.3: Composition change over time expressed as mean and standard error for overall turnover (TTO Jaccard) and both turnover components (TTO_{rich}, TTO_{rep}) before and after one to five years of treatment application. The colors indicate data from control (black) and the three treatments grazer exclusion (red), nutrient addition (green) and nutrient addition plus grazer exclusion (blue). The error bars indicate 95% confidence intervals.

Fig.4: Composition changes in form of species replacement (TTO rep) and species richness change (TTO rich) after five years of treatment application. The colors indicate changes in the control (black) and the three treatment plots, i.e. grazer exclusion (red), nutrient addition (green) and nutrient addition plus grazer exclusion (blue). The bars represent standard errors of both turnover components. The grey line represents constant total change (Jaccard, control plots) indicating the possible paired contributions of both turnover components.