**Eutrophication reduces the insurance of biodiversity on stability across spatial scales**

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**Abstract**

**Eutrophication usually reduces the diversity and stability of local plant communities. However, the cascading effects of chronic fertilization at larger spatial scales that are most relevant to policy and conservation remain unknown. Here, we quantified such cascading effects from communities to metacommunities across 48 grasslands worldwide. Unmanipulated communities with more plant species had greater asynchrony among species and greater stability of species, resulting in greater stability of community function. Moreover, unmanipulated communities with more even abundances of species and greater variation in composition had greater spatial asynchrony among local communities, resulting in greater stability of metacommunity function. Fertilization reduced the contribution of plant diversity on these mechanisms promoting stability, thus diminishing the local and spatial insurance of biodiversity on stability across spatial scales. Our findings suggest that preserving grassland stability requires conservation of high diversity within and among ecological communities. Furthermore, they demonstrate the threat of fertilization to the stable provisioning of grassland services across spatial scales under current and future environmental changes.**

**Introduction**

Humans are altering the global nutrient cycles via combustion of fossil fuels, fertilizer application and atmospheric deposition (Galloway et al. 2008, Erisman et al. 2013). We have more than doubled the pre-industrial rate of N supply to terrestrial ecosystems, and global P liberation (Carpenter et al. 1998, Vitousek et al. 2002, Galloway 2005), and anthropogenic terrestrial N and P inputs are predicted to reach levels that are three to four times the pre-industrial rates by 2050 (Tilman 1999b, Tilman et al. 2001). The impacts of this eutrophication on terrestrial and aquatic ecosystems are manifold. In grasslands, nutrient enrichment usually increases primary productivity, leads to plant communities composed by a few dominant exploitative species, causes a loss of plant diversity, and reduces the temporal stability of ecosystem functioning (Hautier et al. 2014, Xu et al. 2015, Zhang et al. 2016, Soons et al. 2017).

Concerns that eutrophication may affect ability of ecosystems to provide reliable functions and services for humanity have led to a growing number of theoretical and empirical studies investigating how these ecosystem responses may be mechanistically linked (Grman et al. 2010, Yang et al. 2012, Thibaut and Connolly 2013, Hautier et al. 2014, Hautier et al. 2015, Zhang et al. 2016). Previous studies, primarily focusing on relatively small spatial scales (i.e. study plots or local communities), have shown that fertilization can reduce the stability of community productivity through a reduction of plant diversity (but see Hautier et al. 2014, Liu et al. 2019), a decrease of species stability, and a decline in the degree of asynchronous dynamics among species. However, the cascading effects of fertilization on ecosystem stability at larger spatial scales that are most relevant to policy and land management remain unknown.

The recent theoretical development of a hierarchical framework allows for the quantification of such cascading effects from local to larger spatial scales - from communities to metacommunities (Fig. 1) (Wang and Loreau 2014, 2016, Wang et al. 2019). At the community level, higher temporal stability of community function (alpha stability), defined here as the temporal mean of an ecosystem function (e.g. primary productivity) divided by its temporal standard deviation (Tilman 1999a), can result from higher average stability of all species (species stability) and a higher degree of asynchronous dynamics among species (species asynchrony). At the metacommunity level, higher stability of the metacommunity function (gamma stability) can result from higher alpha stability and a higher degree of asynchronous dynamics across local communities (spatial asynchrony, a.k.a. beta stability). Thus, the stabilizing effect of spatial asynchrony on metacommunity function (spatial insurance hypothesis) (Loreau et al. 2003) mirrors the stabilizing effect of species asynchrony on community function (species or local insurance hypothesis) (Lamy.2019.Ecology, Loreau and de Mazancourt 2013, Thibaut and Connolly 2013,Wang & Loreau 2016). Higher species asynchrony and species stability can result from higher local diversity (alpha diversity) through higher number of species within communities (species richness) (Hautier et al. 2015, Wilcox et al. 2017), or through higher evenness in the abundances of species within communities (evenness) (Mikkelson et al. 2011, Thibaut and Connolly 2013). Higher spatial asynchrony can result from higher variation in species composition among communities (beta diversity) (McGranahan et al. 2016)(Wang & Loreau 2016).

According to this framework, the cascading impacts of nutrient inputs on temporal stability can result from changes in plant diversity and asynchronous dynamics at multiple spatial scales (Fig. 1). Chronic increase in the supply of multiple limiting resources could decrease microhabitat heterogeneity and variation in local plant community structure (potentially reducing beta diversity and spatial asynchrony), eliminate species competitive trade-offs contributing to coexistence (potentially reducing alpha and beta diversity), diminish compensatory dynamics among species driven by competition for resources (potentially reducing species asynchrony and species stability), and offset asynchronous responses of species to environmental variability (potentially reducing species asynchrony and species stability) (Ives et al. 1999, Thebault and Loreau 2005, Gonzalez and Loreau 2009). Additionally, nutrient inputs may affect stability by changing the relationships of diversity with asynchrony and stability at multiple spatial scales. Eutrophication may weaken the positive effect of alpha diversity on alpha stability through a decrease in the relationship of alpha diversity with species asynchrony and/or species stability (Hautier et al. 2014, Zhang et al. 2016). Similarly, fertilization may reduce the positive effect of beta diversity on gamma stability through a decrease in the relationship of beta diversity with spatial asynchrony. While elevated nutrient supply has been shown to reduce alpha diversity (Harpole and Tilman 2007, Harpole et al. 2016, Harpole et al. 2017, Kimmel et al. 2019) and the alpha diversity-stability relationship (Hautier et al. 2014, Zhang et al. 2016), its role in mediating the functional consequences of biodiversity changes (variations in the number, abundance and identities of species) and compensatory mechanisms (variations and compensations in species responses) that can scale up to affect the stable provisioning of ecosystem functions at larger spatial scales remains to be elucidated.

To our knowledge, only one recent study has assessed the cascading effect of nutrient enrichment on stability at larger spatial scales (Zhang et al. 2019). That study found that five years of chronic nitrogen addition reduced community stability through a reduction of plant species richness and a decline of species asynchrony. In contrast, spatial asynchrony was not affected by nitrogen addition, suggesting that spatial insurance effects can stabilise ecosystems at larger spatial scales in response to environmental changes. However, these conclusions were based on a single grassland site manipulating a single nutrient, with the implicit assumption that the relationship between diversity and stability was unaffected by eutrophication. This questions the generality of the mechanistic links between these ecosystem responses under eutrophication.

Here, we used bivariate analyses and advanced statistical modelling approaches applied to a large-scale coordinated, multi-year data collection to assess the cascading impact of eutrophication on biodiversity, asynchrony and stability across spatial scales. Using structural equation modelling (SEM) (Grace et al. 2012), we evaluated multiple hypotheses related to key predictions from theories (Table S1). Samples were collected using a globally-coordinated nutrient enrichment experiment conducted across 48 unmanipulated and 48 fertilized metacommunities from 48 grassland sites on six continents (Nutrient Network, Borer et al. 2013). We selected data from sites that had a minimum of four and a maximum of nine years of experimental duration (hereafter ‘period of experimental duration’, Table S2). Sites spanned a broad envelope of seasonal variation in precipitation and temperature (Figure S1) and a wide range of grassland types (Table S2). Each site used standardized methods to quantify plant diversity, asynchronous dynamics and temporal stability at multiple spatial scales in both unmanipulated controls and experimentally fertilized plots with nitrogen, phosphorus and potassium and micronutrients added in combination (NPK) in a well-replicated design (see Methods) (Borer et al 2016). For each site and treatment, the metacommunity consisted of three communities (three replicated blocks per treatment and site). Previous NutNet analyses have shown that while local unmanipulated and fertilized communities slowly diverge over time, plant species are able to colonize from all the plots, thus showing that our meta-communities are linked by dispersal (Hodapp et al. 2018). Variables measured at the local community scale included alpha diversity (average species richness and evenness), species stability (average stability of all species), species asynchrony (asynchronous dynamics among species), and alpha stability (temporal stability of community function). Variables measured at the larger metacommunity scale included beta diversity (abundance- and richness-based multiplicative partitioning of gamma diversity), spatial asynchrony (asynchronous dynamics among communities), and gamma stability (temporal stability of metacommunity function) (see methods). The SEM model shown in Fig. 1e was evaluated separately for each period of experimental duration and treatment and an autoregressive meta-analysis was performed to estimate effect sizes for SEM’s paths across time for each treatment. We assessed the effects of eutrophication on stability both through changes in the relationship of diversity with asynchrony and stability and through changes in diversity. Because plant diversity, asynchronous dynamics and temporal stability may be jointly controlled by inter-annual climate variability, we ran similar analyses on the residuals of models that included the coefficient of variation among years for each of temperature and precipitation (see Methods).

**Results and discussion**

Bivariate analyses revealed negative impacts of nutrient inputs on biodiversity-stability relationships across spatial scales (Fig. 2; Table S3). Relationships were generally consistent across the different periods of experimental duration considered (Table S3). Fertilization reduced the relationships of plant species richness and evenness with both alpha and gamma stability, and decreased the relationship of beta diversity with both beta stability (spatial asynchrony among local communities) and gamma stability. Richness was positively associated with alpha and gamma stability in the unmanipulated communities (Fig. 2a-b), but unrelated in the fertilized communities (Fig. 2c-d). Evenness was unrelated with alpha stability and positively related with gamma stability in the unmanipulated communities (Fig. 2e-f), but negatively associated with both alpha and gamma stability in the fertilized communities (Fig. 2g-h). Beta diversity was positively related to beta and gamma stability in the unmanipulated communities (Fig. 2i-j), but unrelated to beta and gamma stability in the fertilized communities (Fig. 2k-l). These relationships remained when accounting for variation in climate using residual regression (Fig. S2), using biomass estimates instead of percentage cover (Fig. S3), and using 23 sites with a full nine years of treatment application (Fig. S4). To our knowledge, our study is the first to report the positive association between evenness and gamma stability in real-world grasslands, and the negative impacts of fertilization on the relationship of evenness and beta diversity with stability at the two scales considered.

SEM analyses provided strong evidence that species stability, species asynchrony and spatial asynchrony are key mechanisms mediating the relationships of alpha and beta diversity with alpha and gamma stability under unmanipulated conditions and that fertilization disrupts the positive contribution of biodiversity on each of these mechanisms across spatial scales (Fig. 3; Table 1; Fig. S5).

Greater alpha and gamma stability at higher plant species richness in the unmanipulated communities (Fig. 2a-b) resulted predominantly from more asynchronous dynamics among species (standardized path coefficient = 0.34), a path that was generally positive for each period of experimental duration considered (significant in separate SEM based on six years of post-treatment, and marginally significant based on four, seven, eight and nine years), and to a much lower extent from greater species stability (standardized path coefficient = 0.07; a path that was never significant in separate SEMs) in richer communities (Fig. 3a; Fig. S2). The positive association between richness and alpha stability is consistent with experimental (Tilman et al. 2006, Bezemer and van der Putten 2007, Isbell et al. 2009, Hector et al. 2010) and shorter-term observational evidence (Tilman 1996, Bai et al. 2004, Hautier et al. 2014). Our results confirm the substantial role of species asynchrony and to a lesser extent species stability as mechanisms promoting local stability in naturally-assembled species-rich grassland communities (Hautier et al. 2014, Zhang et al. 2016, Zhang et al. 2019). Furthermore, our results are the first to establish the general stabilizing role of plant richness across spatial scales.

Fertilization reduced the positive effects of plant species richness on alpha and gamma stability (Fig. 2a,c and b,d) via a combination of two processes (Fig. 3b; Fig. S2). First, while richness was positively related to species asynchrony in the fertilized communities, this effect was much weaker than in the unmanipulated communities (standardized path coefficient = 0.18; a path that was never significant in separate SEMs). Second, this positive effect was counteracted by a negative relationship of richness with species stability (standardized path coefficient of indirect effect = -0.10; a path that was never significant in separate SEMs), explaining the overall weaker alpha stability at higher richness with fertilization. Our results extend previous evidence obtained over shorter experimental periods in which fertilization consistently weakened the positive effect of richness on community stability through a reduction in species asynchrony and species stability (Hautier et al. 2014, Zhang et al. 2016, Zhang et al. 2019). Our study is the first to show that these negative effects cascade to larger spatial scales. Nutrient enrichment often reduces plant richness (Stevens et al. 2004, Hautier et al. 2009), which could in turn reduce species asynchrony and local stability (Tilman et al. 2006, Hector et al. 2010, Hautier et al. 2015). However, while nutrient enrichment reduced species richness (by an average of 1.5 species), our experiment did not show the expected loss of local stability following loss of species (Fig. S6), confirming results from other studies (Xu et al. 2015, Zhang et al. 2016, Liu et al. 2019) and earlier NutNet results obtained over shorter time periods (Hautier et al. 2014). This could be because negative feedback of nutrient-induced loss of richness on stability require longer experimental duration to manifest (Isbell et al. 2013, Hautier et al. 2015)(Seabloom et al. ANPP-div feedback paper).

Theoretical studies have suggested that evenness may increase or decrease community stability, depending on its combined effects on species asynchrony and species stability (Thibaut and Connolly 2013). Higher evenness may decrease alpha stability by decreasing the dominance of highly stable species (Polley et al. 2007), or increase alpha stability by providing a greater likelihood for asynchronous fluctuations among species to compensate one another when species abundances within communities are more equal (Doak et al. 1998, Loreau 2010). In agreement with experimental results (van Ruijven and Berendse 2007, Isbell et al. 2009), we provide unique evidence of the lack of relationship between evenness in species abundances and community stability within naturally assembled plant communities (Fig. 2e). Furthermore, we show that the absences of this relationship was the product of the non-significant relationships of evenness with species asynchrony and species stability (Fig. 3a; Fig. S2).

Fertilization reduced the strength of the relationship of evenness with alpha stability (Fig. 2e,g) through a strong negative relationship between evenness and species stability (standardized path coefficient = -0.43), a pathway that was generally negative for each period of experimental duration considered (significant in separate SEM based on four, five, six and eight years of post-treatment and marginally significant based on the other periods) (Fig. 3b; Fig. S2). This result suggests that fertilization reduced alpha stability at high evenness by increasing the variability of dominant species to environmental fluctuations. This could in part be explained by nutrient-induced reduction of evenness (by an average of 0.03), which in turn reduced species stability and alpha stability (Fig. S6).

Greater gamma stability at higher evenness in the unmanipulated communities (Fig. 2f) resulted from higher degree of asynchronous dynamics among local communities (standardized path coefficient = 0.38), a pathway that was generally positive for each period of experimental duration considered (significant in separate SEM based on seven, eight and nine years of post-treatment and marginally significant based on five and six years) (Fig. 3a; Fig. S2). This suggests that landscapes composed of local communities with a more equitable distribution of species abundances provide greater opportunities for asynchronous fluctuations between communities to compensate one another and stabilize functioning at larger spatial scales. This could be because, when evenness is low, community dynamics across localities are driven by a few very abundant species that are more likely to respond similarly to environmental fluctuations, compared with when evenness is high. In contrast, fertilization reduced the strength of the relationship between evenness and gamma stability (Fig. 2f,h) through a reduction of the relationship between evenness and spatial asynchrony (standardized path coefficient = 0.08) (Fig. 3b; Fig. S2). Thus, fertilization increased similarity in community dynamics across localities in more even communities. One potential explanation is that fertilization causes more even local communities to be increasingly dominated by species best suited to the novel environmental conditions, resulting in lower spatial asynchrony and thereby gamma stability (Thibaut and Connolly 2013).

Greater gamma stability at higher beta diversity in the unmanipulated communities (Fig. 2j) resulted from higher degree of asynchronous dynamics among local communities (standardized path coefficient of indirect effect = 0.30), a pathway that was generally positive for each period of experimental duration considered (significant in separate SEM based on five, six and seven years of post-treatment and marginally significant based on eight years) (Fig. 3a; Fig. S2). While theoretical studies have suggested the role of beta diversity in driving spatial asynchrony (Wang and Loreau 2014, 2016), previous empirical studies conducted at a single site along a nitrogen gradient (Zhang et al. 2019) or across 62 sites with non-standardized protocols (Wilcox et al. 2017) did not find an association between these two variables. Here, we show that the presence of different species among local communities is linked to higher variation in dynamics among them, thus demonstrating the stabilizing role of beta diversity at larger spatial scales through spatial asynchrony. In contrast, nutrient enrichment reduced the strength of the relationship between beta diversity and gamma stability (Fig. 2j,l) through a reduction of the relationship between beta diversity and spatial asynchrony (standardized path coefficient = 0.10) (Fig. 2i,k; Fig. 3a; Fig. S2). This result provides strong evidence that fertilization can reduce the stabilizing role of spatial asynchrony in dissimilar communities at larger spatial scales. We did not find evidence that this was due to negative feedback of nutrient-induced loss of beta diversity on stability (Fig. S6). The positive relationship between beta diversity and spatial asynchrony, and the negative impact of fertilization on that relationship, suggest that high microhabitat heterogeneity and variation in species composition among local communities that buffer local community responses to environmental fluctuations are disrupted under nutrient enrichment.

In agreement with previous studies (Wilcox et al. 2017, Polley and Wilsey 2018, Zhang et al. 2019), we found that alpha stability contributed relatively more to gamma stability compared to spatial asynchrony (Fig. 3a). This suggests that preserving or restoring local plant diversity and its associated positive contribution to species asynchrony and alpha stability will provide stronger insurance against environmental fluctuations at larger spatial scales than diversifying the landscape. However, in these studies, the relatively small number of communities within metacommunities as compared to the usually high number of species within communities, are likely to diminish the potential for compensatory mechanisms among communities to contribute to gamma stability as compared to those within communities. Indeed, separate SEMs show that the relative contribution of alpha stability increased while the relative contribution of spatial asynchrony decreased with increasing duration of the study (Fig. S7a). The lower relative contribution of spatial asynchrony over time could be due to the fact that a lower number of metacommunities (sites) are included in the analyses with increasing duration of the study. Results of separate SEM analyses conducted over the longest duration (nine year) and keeping the number of metacommunities equal (23) for each period of experimental duration confirmed the increasing contribution of alpha stability on gamma stability over time for comparable contribution of spatial asynchrony (Fig. S4b). Additionally, the relative contribution of spatial asynchrony and beta diversity to gamma stability should increase with spatial heterogeneity in soil nutrients and environmental conditions which would be best captured by studying metacommunities across larger spatial scales than the ones considered in these studies. Future research could more completely determine the relative contribution of alpha stability and spatial asynchrony to gamma stability by simultaneously varying the number and abundances of species within communities, the number of communities within metacommunities, and the duration and spatial extent of the study.

We explored the drivers of temporal stability across spatial scales in unmanipulated and fertilized plant communities worldwide. The results of our study show that greater alpha and gamma stability at higher richness resulted from greater asynchronous dynamics among species and greater stability of species in species-rich communities, thus conferring local insurance against environmental fluctuations. Furthermore, they show that greater spatial asynchrony resulted from greater evenness within communities and greater beta diversity, thus conferring spatial insurance against environmental fluctuations. Eutrophication reduced the contribution of diversity on each of the mechanisms promoting stability at the local and larger spatial scale, thus diminishing the local and spatial insurance of biodiversity on stability. Additionally, while eutrophication reduced species richness, and evenness, only changes in evenness in response to eutrophication resulted in reduced species stability. Our results demonstrate that stability across spatial scales is driven by a combination of direct and indirect effects through changes in diversity and asynchrony. Preserving ecosystem stability across spatial scales therefore requires preservation and restoration of diversity and species evenness within local communities, as well as creation and maintenance of the habitat or microhabitat heterogeneity that preserves spatial variability across local communities. Moreover, conservation policies and management procedures that prevent eutrophication need to be developed in order to preserve the insurance provided by biodiversity on stability across scales against current and future environmental changes.

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