Received: 20 July 2021 | Accepted: 1 January 2022

DOI: 10.1111/gcb.16086

Global Change Biology WILEY

RESEARCH ARTICLE

# Nutrients and herbivores impact grassland stability across spatial scales through different pathways

Qingqing Chen[1] | Shaopeng Wang[1] | Eric W. Seabloom[2] | Andrew S. MacDougall[3] | Elizabeth T. Borer[2] | Jonathan D. Bakker[4] | Ian Donohue[5] | Johannes M. H. Knops[6] | John W. Morgan[7] | Oliver Carroll[3] | Mick Crawley[8] | Miguel N. Bugalho[9] | Sally A. Power[10] | Anu Eskelinen[11,12,13] | Risto Virtanen[13] | Anita C. Risch[14] | Martin Schütz[14] | Carly Stevens[15] | Maria C. Caldeira[16] | Sumanta Bagchi[17] | Juan Alberti[18] | Yann Hautier[19]

[1]Institute of Ecology, College of Urban and Environmental Sciences, and Key Laboratory for Earth Surface Processes of the Ministry of Education, Peking University, Beijing, China

[2]Department of Ecology, Evolution, and Behavior, University of Minnesota, St. Paul, Minnesota, USA

[3]Department of Integrative Biology, University of Guelph, Guelph, Ontario, Canada

[4]School of Environmental and Forest Sciences, University of Washington, Seattle, Washington, USA

[5]Department of Zoology, School of Natural Sciences, Trinity College Dublin, Dublin, Ireland

[6]Department of Health and Environmental Sciences, Xi'an Jiaotong liverpool University, Suzhou, China

[7]Department of Ecology, Environment & Evolution, La Trobe University, Bundoora, Victoria, Australia

[8]Life Sciences, Imperial College London, Silwood Park, Ascot, UK

[9]Centre for Applied Ecology "Prof. Baeta Neves" (CEABN-InBIO), School of Agriculture, University of Lisbon, Lisbon, Portugal

[10]Hawkesbury Institute for the Environment, Western Sydney University, Penrith, New South Wales, Australia

[11]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany

[12]Department of Physiological Diversity, Helmholtz Centre for Environmental Research - UFZ, Leipzig, Germany

[13]Department of Ecology and Genetics, University of Oulu, Oulu, Finland

[14]Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Birmensdorf, Switzerland

[15]Lancaster Environment Centre, Lancaster University, Lancaster, UK

[16]Forest Research Centre, School of Agriculture, University of Lisbon, Lisbon, Portugal

[17]Centre for Ecological Sciences, Indian Institute of Science, Bangalore, India

[18]Instituto de Investigaciones Marinas y Costeras (IIMyC), FCEyN, UNMdP-CONICET, Mar del Plata, Argentina

[19]Ecology and Biodiversity Group, Department of Biology, Utrecht University, Utrecht, The Netherlands

**Correspondence**
Shaopeng Wang, Institute of Ecology, College of Urban and Environmental Sciences, and Key Laboratory for Earth Surface Processes of the Ministry of Education, Peking University, 100871 Beijing, China.
Email: shaopeng.wang@pku.edu.cn

**Funding information**
National Natural Science Foundation of China: 31988102, 32122053; National Science Foundation, Grant/Award Number: NSF-DEB-1042132, NSF-DEB-1234162 and NSF-DEB-1831944; Institute on the Environment (DG-0001-13).

## Abstract

Nutrients and herbivores are well-known drivers of grassland diversity and stability in local communities. However, whether they interact to impact the stability of aboveground biomass and whether these effects depend on spatial scales remain unknown. It is also unclear whether nutrients and herbivores impact stability via different facets of plant diversity including species richness, evenness, and changes in community composition through time and space. We used a replicated experiment adding nutrients and excluding herbivores for 5 years in 34 global grasslands to explore these questions. We found that both nutrient addition and herbivore exclusion alone reduced stability at the larger spatial scale (aggregated local communities; gamma

stability), but through different pathways. Nutrient addition reduced gamma stability primarily by increasing changes in local community composition over time, which was mainly driven by species replacement. Herbivore exclusion reduced gamma stability primarily by decreasing asynchronous dynamics among local communities (spatial asynchrony). Their interaction weakly increased gamma stability by increasing spatial asynchrony. Our findings indicate that disentangling the processes operating at different spatial scales may improve conservation and management aiming at maintaining the ability of ecosystems to reliably provide functions and services for humanity.

**KEYWORDS**
biodiversity-stability, cross-scale, eutrophication, grazing, Nutrient Network (NutNet)

## 1 | INTRODUCTION

Quantifying the temporal stability of ecosystems has been a central quest in ecology as it informs on the ability of an ecosystem to provide consistent functions and services despite environmental perturbations. Nutrient enrichment and herbivore loss are two significant global change factors that are happening simultaneously in grassland ecosystems (Atwood et al., 2020; Galloway et al., 2004). Eutrophication induced by fossil fuels and fertilizer application is predicted to increase terrestrial N and P inputs by three times of the preindustrial rates by 2050 (Tilman et al., 2001). Meanwhile, herbivores, especially wild large herbivores, are decreasing dramatically due to hunting and habitat destruction (Ripple et al., 2019). During the last decades, we have accumulated knowledge about the separate effects of nutrients and herbivores on biodiversity, ecosystem functioning, temporal stability, and the links between them. For instance, nutrient addition often decreases plant diversity and stability in local communities, and these effects may propagate to larger spatial scales (Hautier et al., 2015; Koerner et al., 2016; Liu et al., 2019; Zhang et al., 2019). In contrast, herbivore exclusion has been found to have positive, neutral, or negative effects on grassland plant diversity and stability, depending on the herbivore species excluded and spatial scales studied (Blüthgen et al., 2016; Ganjurjav et al., 2019; Halpern et al., 2005; Hautier et al., 2015; Liu et al., 2021; Qin et al., 2019; Ren et al., 2018; Saruul et al., 2019). A range of studies has also examined the joint effects of nutrients and herbivores on grassland productivity (Alberti et al., 2010, 2011; Borer et al., 2020; Chase et al., 2000; Milchunas & Lauenroth, 1993; Moran & Scheidler, 2002) and plant diversity using either species richness (Alberti et al., 2010, 2011; Bakker et al., 2006; Beck et al., 2015; Borer et al., 2014b; Hillebrand et al., 2007; Koerner et al., 2018; Proulx & Mazumder, 1998; Worm et al., 2002; Yang et al., 2013), community evenness (Hillebrand et al., 2007), or community composition (Alberti et al., 2017; Chase et al., 2000; Grellmann, 2002; Hartley & Mitchell, 2005; Hodapp et al., 2018; Milchunas & Lauenroth, 1993). The majority of these studies found strong interactive effects of nutrients and herbivores. However, to our knowledge, no study has investigated how nutrients and herbivores jointly regulate the stability of aboveground biomass across multiple spatial scales in grasslands across the world.

Conservation and management usually focus on large spatial scales (e.g. landscape); it is, therefore, important to scale up our understanding of the effects of nutrients and herbivores on stability from local to larger spatial scales (Isbell et al., 2017). Stability is a multidimensional concept (Donohue et al., 2013). Here, we use temporal stability, defined as the temporal invariability, calculated as the mean of aboveground biomass through time divided by its standard deviation in local communities (alpha stability) and at the larger spatial scales (aggregated local communities; gamma stability). Because plant biomass in grasslands provides food for wild animals, livestock, and humans, high temporal variability of plant biomass production may endanger food security and lead to ecosystem collapse (Macdougall et al., 2013). Understanding the mechanisms and processes by which nutrients and herbivores jointly impact the stability of aboveground biomass across spatial scales can, therefore, provide useful recommendations for conservation and management.

Nutrients and herbivores may impact stability across spatial scales through multiple facets of plant diversity including species richness, evenness, and community dissimilarity across time and space. Recent theory suggests that gamma stability can be partitioned into alpha stability of local communities and asynchronous dynamics among local communities (i.e. spatial asynchrony; Wang et al., 2019). Thus, nutrients and herbivores can impact gamma stability through changing alpha stability and/or spatial asynchrony. On the one hand, nutrient addition and herbivore exclusion may decrease alpha stability by decreasing alpha diversity (i.e. species richness in local communities) and evenness or by increasing temporal community dissimilarity (Grman et al., 2010; Koerner et al., 2016; Liang et al., 2021). Increased nutrients or reduced disturbances from herbivores may enhance interspecific competition, leading to increased local dominance, reduced evenness and alpha diversity, and increased temporal community dissimilarity (Chen et al., 2019, 2021; Tilman, 1987). Decreased alpha diversity and evenness may decrease alpha stability due to reduced compensatory dynamics between species (Gonzalez & Loreau, 2009; Hector

et al., 2010). On the other hand, nutrient addition and herbivore exclusion may affect spatial asynchrony through changing spatial beta diversity and community dissimilarity (Liang et al., 2021; Wang et al., 2021). Spatial beta diversity emphasizes rare and abundant species equally, whereas spatial community dissimilarity emphasizes abundant species. Increased nutrients and decreased disturbances from herbivores may decrease spatial beta diversity and community dissimilarity by homogenizing biotic and abiotic environments (Adler et al., 2001; Molina et al., 2021), or increase them by promoting stochasticity in local community assemblage (Alberti et al., 2017; Chase, 2010). Moreover, nutrients and herbivores may have synergistic effects on stability due to their interactive effects on plant diversity facets. For instance, herbivore exclusion may decrease alpha diversity more under high- than low-nutrient conditions because nutrient addition may promote dominance of fast-growing, highly nutritious plant species that attract more herbivores (Endara & Coley, 2011). Thus, the effects of herbivore exclusion on stability may be stronger under higher nutrient conditions.

Temporal and spatial community dissimilarity integrate both changes in species identities and their abundances across time and space; thus, they may predict stability across spatial scales better relative to alpha and beta diversity (Lamy et al., 2021). Here, we use species cover as a measure of abundance. Community dissimilarity across time or space can arise from two concurrent processes, namely abundance gradients and balanced variation in abundance (Baselga, 2017). Abundance gradients arise from a simultaneous increase or decrease in the cover of each species, leading to gradients in total cover (e.g. some years or places are subsets of others). Balanced variation arises from replacement among species. That is, decreases in the cover of some species in some years or places are compensated for by increases in other species in other years or places. A previous study using global grasslands shows that nutrient addition and herbivore exclusion alone increase community composition (in occurrence) change over time more through species replacement rather than through species loss or gain (Hodapp et al., 2018). Similarly, nutrient addition and herbivore exclusion may impact temporal and spatial community dissimilarity primarily through driving changes in balanced variation rather than abundance gradients. An increase in temporal community dissimilarity driven by balanced variation may decrease alpha and gamma stability. This is because even if the total cover does not vary, changes in dominant species may change ecosystem functioning and stability (Winfree et al., 2015). In comparison, an increase in spatial community dissimilarity driven by spatial balanced variation may increase spatial asynchrony due to compensatory dynamics among local communities (Wang & Loreau, 2016), thereby increasing gamma stability.

Assessing the relative contribution of different facets of plant diversity to alpha and gamma stability can deepen our understanding of the role of plant diversity facets in maintaining ecosystem stability and help prioritize conservation efforts. For instance, should management focus on the maintenance of a higher number of plant species or the identities of the species within or among local communities? Our understanding of the effects of plant diversity on stability remains limited because studies often focus on some particular facets of plant diversity and rarely assessed multiple facets of plant diversity together (Grime, 1998; Grman et al., 2010; Hautier et al., 2015; Koerner et al., 2016; Polley et al., 2007; Tilman et al., 2006; but see Craven et al., 2018). Therefore, it remains unclear which plant diversity facets mediate the effects of nutrients and herbivores on stability across spatial scales.

Here, we used a globally coordinated grassland experiment, Nutrient Network (NutNet) to answer the following three questions. First, does nutrient addition and herbivore exclusion interact to impact the temporal stability of aboveground biomass at the local and larger spatial scales (i.e. alpha and gamma stability)? Second, what is the relative contribution of different facets of plant diversity including alpha and beta diversity, evenness, temporal and spatial community dissimilarity in mediating the treatment effects on alpha and gamma stability? Third, which components of temporal and spatial community dissimilarity impact alpha and gamma stability? We hypothesize that (1) nutrient addition and herbivore exclusion alone decrease alpha and gamma stability, and the effects of herbivore exclusion may be stronger under higher nutrient conditions; (2) the decrease in gamma stability is due to a reduction in alpha stability and spatial asynchrony, which are primarily regulated by temporal and spatial community dissimilarity; and (3) balanced variation contributes more to temporal and spatial community dissimilarity than abundance gradients. Whereas increased temporal balanced variation decreases alpha and gamma stability, increased spatial balanced variation increases spatial asynchrony and gamma stability.

## 2 | MATERIALS AND METHODS

### 2.1 | Experimental design

We replicated a factorial combination of nutrient addition and herbivore exclusion by fencing at 34 sites, which were part of the NutNet distributed experiment (Borer et al., 2014a). These sites were the subset of sites that met the following criteria: (1) with 5 years of posttreatment measurement; (2) with three blocks; for a few sites with more than three blocks, we selected the first three blocks following Hautier et al. (2020); and (3) each block contains a factorial design of nutrient addition and herbivore exclusion by fencing. A block typically spreads over 320 $m^2$, and all three blocks typically spread over >1000 $m^2$. These sites span over four continents and include a wide range of grassland types such as montane, alpine, semiarid grasslands, prairies, old fields, pastures, savanna, tundra, and shrub-steppe. See Table S1 for details for sites selected, experimental years used, and their geolocation.

Within each block at each site, four treatments (control, Fence, NPK, and NPK + Fence) were implemented in four 5 × 5 $m^2$ plots (one plot for each treatment). Plots were randomly placed within

a block. NPK and NPK + fence treatments were fertilized with nitrogen (N), phosphorus (P), potassium ($K_{+\mu}$); +μ refers to micronutrients (Fe, S, Mg, Mn, Cu, Zn, B, and Mo in combination) as part of the potassium addition. The micronutrient mix was only applied once at the start of the experiment at a rate of 100 g $m^{-2}$. N was supplied as time-release urea ($(NH_2)_2CO$). P was supplied as triple superphosphate ($Ca(H_2PO_4)_2$), and K as potassium sulfate ($K_2SO_4$). Nutrients were added annually at rates of 10 g $m^{-2}$ $year^{-1}$ for N, P, and K. Ammonium nitrate was used as the nitrogen source in 2007, however, urea was used in all subsequent years due to difficulties in procuring ammonium nitrate (Seabloom et al., 2013). An additional experiment at four NutNet sites shows that ammonium nitrate and urea have similar effects on plant diversity and biomass. Fence and NPK + Fence treatments were enclosed with fences to test the effects of herbivore exclusion (excluding mammalian herbivores >50 g) on plant communities. Fences were around 230 cm tall and the lower 90 cm were covered by 1 cm woven wire mesh. To further exclude digging animals such as voles, an additional 30 cm outward-facing flange was stapled to the soil. Four strands of barbless wire were strung at similar vertical distances above the wire mesh. Of the 34 sites, 6 sites deviated from this fence design (Table S1). Wild herbivores such as rodents, lagomorphs, ungulates, marsupials are present at all sites, whereas domestic herbivores such as sheep, yak, goats, and cattle are also present at a few sites (Table S1). Further details on the design are available in Borer et al. (2014b).

## 2.2 | Sampling protocol

All NutNet sites followed standard sampling protocols. A 1 × 1 $m^2$ subplot within each 5 × 5 $m^2$ plot was permanently marked for recording vegetation properties. The number of species, species identity, and their covers were recorded. Species cover (%) was estimated visually for all species in the subplots, the total cover of living plants can exceed 100% for multilayer canopies. Aboveground biomass was measured adjacent to the permanent subplot by clipping all aboveground biomass within two 1 × 0.1 m strips (in total 0.2 $m^2$), which were moved each year to avoid resampling the same location. For shrubs and subshrubs occurring in strips, we collected all leaves and current year's woody growth. Biomass was dried at 60°C (to constant mass) before weighing to the nearest 0.01 g. Dried biomass was multiplied by 5 to estimate grams per square meter. At most sites, cover and biomass were recorded once per year at peak biomass before fertilization. At some sites with strong seasonality, cover and biomass were recorded twice per year to include a complete list of species and follow typical management procedures at those sites. For those sites, the maximum cover for each species and total biomass were used in the following analyses. The taxonomy was adjusted within sites to ensure consistent naming over time. Specifically, when individuals could not be identified as species (7% of the 954 species recorded), they were aggregated at the genus level but referred as "species" for simplicity.

## 2.3 | Plant diversity facets and stability across scales

Following Hautier et al. (2020), we treated each 1 $m^2$ subplot as a "community" and the three replicated subplots under the same treatment across blocks within a site as the "larger-scale" sensu Whittaker (1972) (see an illustration in Figure S1). Plant diversity facets used in this study included alpha diversity, beta diversity, Pielou's evenness, and community dissimilarity. Alpha diversity (S) is the average number of species recorded in the three subplots in each treatment at each site. Beta diversity is calculated as the ratio of gamma diversity and alpha diversity (i.e. multiplicative beta diversity), where gamma diversity is the total number of species recorded in three subplots under the same treatment at each site. Pielou's evenness was calculated as $H/\ln(S)$, where $H$ is Shannon's diversity index (Shannon, 1948).

We calculated temporal and spatial community dissimilarity using Bray–Curtis dissimilarity metrics based on cover data. This index is most suitable for non-normal, multivariate data and is less sensitive to changes in rare species (Anderson & Walsh, 2013). Temporal community dissimilarity of each treatment was calculated as the dissimilarity of a community through the 5-year experimental period and averaged over the three blocks. Similarly, spatial community dissimilarity of each treatment was calculated as the dissimilarity across the three blocks in each treatment each year and averaged over the experimental years. Temporal/spatial community dissimilarity and the partitioning of it into abundance gradients and balanced variation were done using the function "beta.multi.abund" from the R package betapart with the index. family of "Bray" (Baselga & Orme, 2012). Community dissimilarity, abundance gradients, and balanced variation range from 0 to 1, higher values of community dissimilarity indicate that communities are more dissimilar. The sum of abundance gradients and balanced variation is always 1; higher values of balanced variation indicate that community dissimilarity is more induced by species replacement rather than changes in total cover.

Stability at a given spatial scale was calculated as temporal invariability: $\frac{\mu}{\sigma}$, where $\mu$ and $\sigma$ are the mean and standard deviation of aboveground biomass over the experimental years. We present the effects of nutrient addition, herbivore exclusion, and their interaction on the mean and standard deviation of aboveground biomass at the local and larger spatial scales in Figure S2. Alpha stability was the stability of aboveground biomass averaged over three subplots in each treatment at each site; gamma stability was the stability of total aboveground biomass in three subplots in each treatment at each site (Hautier et al., 2020; Wang et al., 2019). To facilitate among-site comparison, we present raw data of alpha and gamma stability in each treatment at each site in Figure S3. Spatial asynchrony was calculated as $\frac{\sum_i \sqrt{w_{ii}}}{\sqrt{\sum_{ij} w_{ij}}}$, where $w_{ij}$ is the temporal covariance of aboveground biomass between local communities $i$ and $j$, and $w_{ii}$ is the temporal variance of aboveground biomass of local community $i$ (Wang et al., 2019). Because temporal trends in aboveground

biomass exist at some sites, we also calculated alpha, gamma stability, and spatial asynchrony after detrending. Specifically, we detrended aboveground biomass at the larger spatial scale, allowing different trends in local communities, so that spatial asynchrony due to contrasting trends among local communities was not eliminated. These variables were calculated using the R function "var.partition" (Wang et al., 2019).

## 2.4 | Statistical analyses

All analyses were performed in R v.4.0.2 (R Core Team, 2020). First, we tested the treatment effects on each facet of plant diversity and stability using linear mixed-effect models with the function "lme" from the R package "nlme" (Pinheiro et al., 2017). In these models, site was a random variable, the main and interactive effects of nutrient addition and herbivore exclusion are the fixed variables. Alpha diversity, alpha stability, spatial asynchrony, and gamma stability were log-transformed to improve normality and homogeneity of variance.

Second, we built a structural equation model (SEM) using the function "psem" from the R package piecewiseSEM (Lefcheck, 2016) to evaluate the direct and indirect effects of nutrient addition, herbivore exclusion, and their interaction on alpha and gamma stability. An initial model was built based on prior knowledge (Figure S4; Gilbert et al., 2020; Grman et al., 2010; Hodapp et al., 2018; Wilcox et al., 2017; Zhang et al., 2019). Rationales for each link in the initial SEM are summarized in Table S2. To fit the SEM, we used the function "lme" with site as a random effect for each component model to test the relative contribution of both treatments and plant diversity facets to stability (see the caption of Figure S4 for an example of model specification). Note, we did not include treatment effects in the component model for gamma stability due to model saturation, as gamma stability was additively partitioned into alpha stability and spatial asynchrony at the logarithmic scale (Wang et al., 2019). We estimated variance inflation for each component model to make sure that multi-collinearity did not affect parameter estimates (variance inflation <4). Alpha stability, spatial asynchrony, and gamma stability were log-transformed to improve normality and homogeneity of variance. We also ran an SEM using the detrended stability; results were qualitatively similar with or without detrending stability (Figures S5 and S6).

Additionally, we checked whether the links between plant diversity facets and stability under nutrient addition and herbivore exclusion were masked by environmental factors. Several studies suggest that abiotic variables such as rainfall and soil parameters can impact grassland stability (García-Palacios et al., 2018; Gilbert et al., 2020; Zelikova et al., 2014). We, therefore, included temporal variation in standardized water balance (sd.SPEI; account for both precipitation and potential evapotranspiration) in the SEM. SPEI data were extracted from http://hdl.handle.net/10261/202305. SPEI data were aggregated over 12 months prior to the peak biomass harvest from 1902 to 2018 at each site and were standardized to have a mean of 0 and a standard deviation of 1. We then calculated the standard deviation of SPEI during the experimental years (two sites have data in 2019, but this year was not considered at these two sites). We fitted an additional SEM by including spatial variability in soil chemistry using 27 sites where soil chemistry data are available. Previous studies find that grazing intensity may mediate treatment effects on aboveground biomass (e.g. Borer et al., 2020), we thus performed another SEM including grazing intensity using 33 sites where grazing intensity data are available. Details in the calculation of spatial variability in soil chemistry and grazing intensity can be found in online supplementary text. Spatial variability in soil chemistry and grazing intensity did not impact any plant diversity facets and stability metrics, so we did not present these results. We present the results with sd.SPEI in the main text because sd.SPEI had significant effects on stability across spatial scales.

Third, we analyzed which component of temporal community dissimilarity was more related to alpha stability and which component of spatial community dissimilarity was more related to spatial asynchrony. We fitted linear mixed-effect models where alpha stability was the response variable, temporal community dissimilarity (or each of its components), and its interaction with the nutrient addition and herbivore exclusion as the fixed variables. Site was a random variable in these models. We fitted similar models for spatial asynchrony. We define that an effect is significant when $p \leq .05$, and marginally significant when $.05 < p < .1$.

## 3 | RESULTS

On average, nutrient addition alone decreased alpha diversity from ca.11 to 9 species $m^{-2}$ and evenness from 0.69 to 0.66 compared with those under ambient conditions (i.e. without nutrient addition and under herbivore grazing), but it did not affect beta diversity. Nutrient addition alone increased temporal community dissimilarity from 0.55 to 0.58, by increasing temporal balanced variation from 0.43 to 0.48 and decreasing temporal abundance gradients from 0.12 to 0.10, whereas it did not affect spatial community dissimilarity and its components. Moreover, nutrient addition alone had no effects on alpha stability and spatial asynchrony but decreased gamma stability from 2.69 to 2.36. Herbivore exclusion alone decreased alpha diversity from ca. 11 to 10 species $m^{-2}$ compared with that under ambient conditions, but it did not affect evenness, beta diversity, temporal and spatial community dissimilarity, and their components. Moreover, herbivore exclusion alone had no effect on alpha stability, but it decreased spatial asynchrony from 1.30 to 1.16 and marginally decreased gamma stability from 2.69 to 2.40. Nutrient addition and herbivore exclusion had no interactive effects on all variables investigated except for spatial asynchrony. That is, herbivore exclusion decreased spatial asynchrony under nutrient addition conditions but not under ambient conditions (Figure 1; see Table S3 for test statistics).

The SEM clarified the direct and indirect effects of nutrient addition, herbivore exclusion, and their interaction on stability

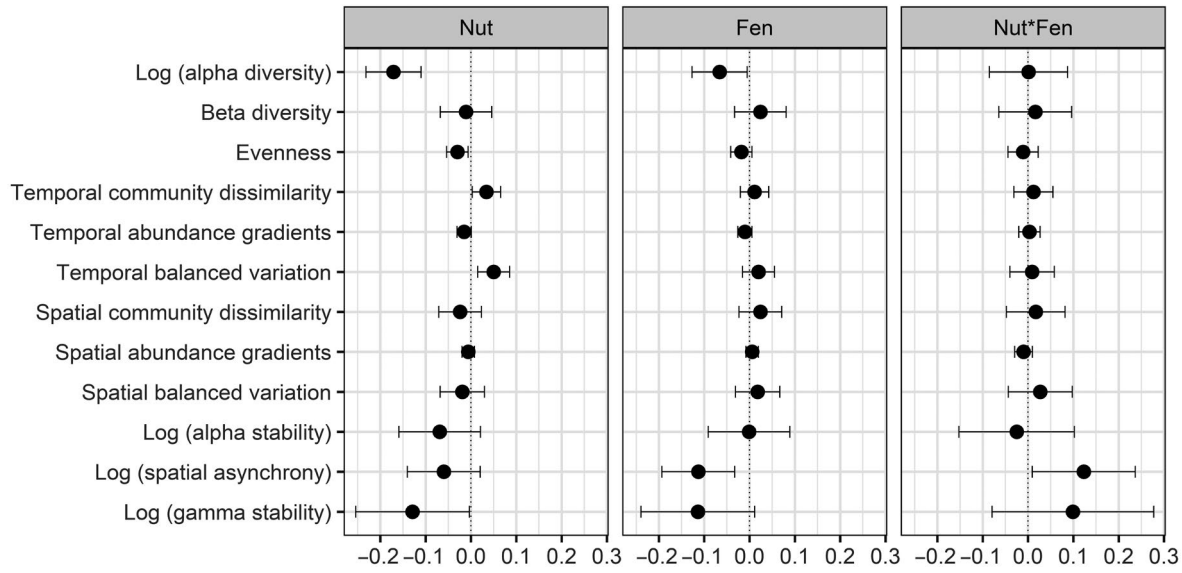


**FIGURE 1** The average response of plant communities ($n = 34$) to nutrient addition, herbivore exclusion by fencing, and their interaction. Nutrient addition (Nut) and herbivore exclusion by fencing (Fen) represent the differences from the ambient plots without nutrient addition and under herbivore grazing. The interaction (Nut * Fen) is relative to the sum of the effects of nutrient addition alone and herbivore exclusion alone. Dots are values estimated from linear mixed-effect models, error bars are 95% confidence intervals. See Table S3 for test statistics

at the local and larger spatial scales. Nutrient addition decreased gamma stability by decreasing alpha stability but not spatial asynchrony. The negative effects of nutrient addition on alpha stability were mediated by increasing temporal community dissimilarity and decreasing evenness, but not through decreasing alpha diversity. In contrast, herbivore exclusion decreased gamma stability by decreasing spatial asynchrony. Their interaction increased gamma stability through increasing spatial asynchrony. Temporal variation in standardized water balance impacted gamma stability through decreasing alpha stability and spatial asynchrony. Importantly, including this environmental factor generally did not alter the links between plant diversity facets and stability (Figure 2; Figure S5).

Lastly, we found that temporal community dissimilarity and temporal balanced variation were negatively related to alpha stability, while temporal abundance gradients were unrelated to alpha stability in all treatments. Spatial community dissimilarity and its components were unrelated to spatial asynchrony in all treatments (Figure 3; see Table S5 for test statistics).

## 4 | DISCUSSION

Using a replicated experiment in 34 global grasslands, we tested the interactive effects of nutrient addition and herbivore exclusion on stability across spatial scales. Our study yields three important findings. First, both nutrient addition and herbivore exclusion alone decreased gamma stability, but through different pathways. Nutrient addition decreased gamma stability through its impacts on alpha stability, which in turn was primarily driven by increasing temporal community dissimilarity. Herbivore exclusion reduced gamma stability primarily by decreasing spatial asynchrony. Second, the interaction of nutrient addition and herbivore exclusion had weak positive effects on gamma stability through increasing spatial asynchrony. Third, community dissimilarities over time and space were both predominantly driven by balanced variation, and the temporal balanced variation was negatively related to alpha stability. Our results highlight that multiple spatial scales should be considered to fully unravel the effects of eutrophication and herbivore loss on ecosystem stability.

Our results suggest that the negative effects of eutrophication and herbivore loss were stronger at the larger spatial scale relative to the local scale. Under nutrient addition, stability decreased by 7% to 12% from alpha to gamma scales, whereas under herbivore exclusion, it decreased by <0.1% to 11% from alpha to gamma scales on average over the 34 sites. Although the average effects of nutrient addition and herbivore exclusion alone on stability were negative, considerable variation exists among sites. At a few sites, herbivore exclusion did not impact stability at both spatial scales studied (e.g. comp.pt, rook.uk, and yarra.au) or herbivore exclusion and nutrient addition even increased stability (e.g. chilcas.ar, kiny.au, saana.fi, and trel.us; Figure S3). At one site (cdpt.us), nutrient addition and herbivore exclusion decreased stability more at the local scale than at the larger scale. We acknowledge that the larger spatial scale (ca. 0.1 ha) used here is still relatively small compared with realistic landscapes that conservation and management typically focus on. It remains an open question how the effects of nutrients and herbivores change as the spatial scale increases further to landscape scales, particularly for herbivores. This is because herbivore effects are often highly dependent on herbivore density, herbivore size, their preference for

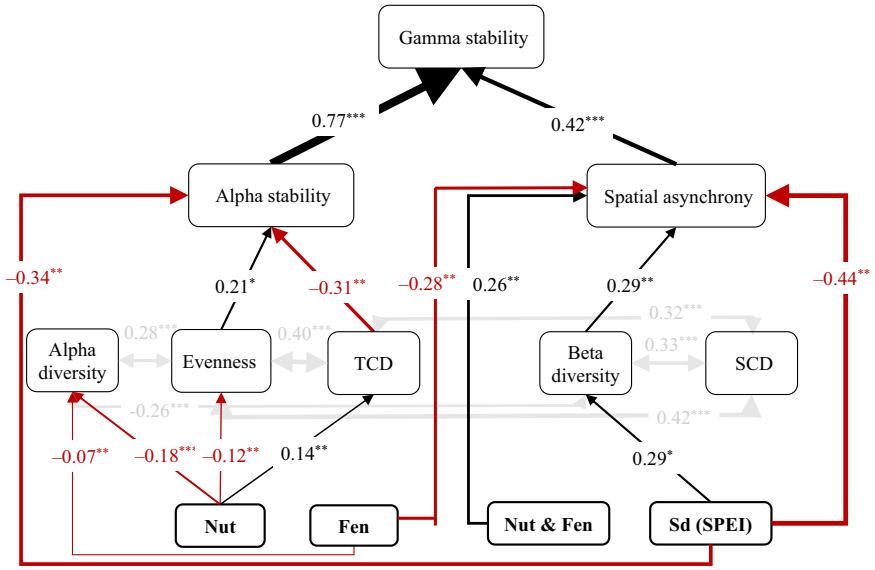


**FIGURE 2** Direct and indirect effects of nutrient addition (Nut), herbivore exclusion by fencing (Fen), and their interaction (Nut * Fen) on stability at the local (i.e. alpha stability) and larger spatial scales (i.e. gamma stability). Model fits the data well (Fisher's $C = 40.603$, $p = .275$, $df = 36$, $N = 136$). Boxes represent measured variables, and arrows represent relationships among variables. The displayed numbers are standardized path coefficients. Width of the arrows indicates the strength of the pathways. Line color represents positive (black) and negative (red) path coefficients. Grey arrows and numbers show correlated errors. Asterisks indicate significant paths: $^{*}p < .1$; $^{**}p \leq .05$; $^{***}p \leq .001$. Nonsignificant paths are not shown. See Table S4 for $R^2$ for each component model. Alpha stability, spatial asynchrony, and gamma stability were on the log scale to improve normality and homogeneity of variance. SCD, spatial community dissimilarity; Sd.SPEI, temporal variation in standardized water balance; TCD, temporal community dissimilarity [Colour figure can be viewed at wileyonlinelibrary.com]

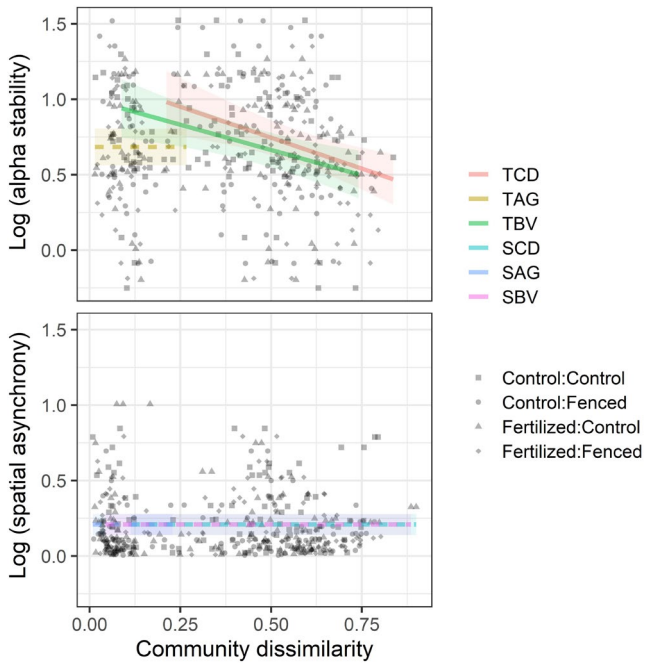


**FIGURE 3** Relationships between community dissimilarity, its components, and alpha stability and spatial asynchrony. Lines are fitted with linear mixed-effect models; shades are 95% confidence bands. Solid lines show significant relationships; dashed lines show nonsignificant relationships. Note, three regression lines overlapped with each other in the lower panel. SAG, spatial abundance gradients; SBV, spatial balanced variation; SCD, spatial community dissimilarity; TAG, temporal abundance gradients; TBV, temporal balanced variation; TCD, temporal community dissimilarity. See Table S5 for model specifications and test statistics [Colour figure can be viewed at wileyonlinelibrary.com]

forage plants, and plant community composition at sites (Adler et al., 2001; Howison et al., 2017). More studies ranging from plot to regional scales in different ecosystems are needed to fully unravel how the effects of nutrients and herbivores on ecosystem stability would change as spatial scale increases.

Importantly, we found that nutrient addition decreased gamma stability through small-scale processes while herbivore exclusion decreased stability through large-scale processes. Nutrient addition probably intensified interspecific competition within local communities, which led to local dominance, decreased evenness and alpha diversity, and increased temporal community dissimilarity (Koerner et al., 2016; Tilman, 1987). However, nutrient addition did not impact alpha and gamma stability through decreasing alpha diversity. This may be because the positive effect of alpha diversity on alpha stability itself was weakened under nutrient addition (Hautier et al., 2020). Instead, we found that temporal community dissimilarity might be a better indicator (compared with alpha diversity and evenness) for alpha stability under nutrient addition (Koerner et al., 2016). Indeed, temporal community dissimilarity is regarded as an index of compositional stability (a higher temporal community dissimilarity corresponds to lower compositional stability; Hillebrand & Kunze, 2020; White et al., 2020). Higher compositional stability usually leads to higher functional stability (e.g. biomass; Allan et al., 2011). In contrast, herbivore exclusion decreased gamma stability mainly through decreasing spatial asynchrony. This is probably because herbivores promote vegetation heterogeneity via selective grazing, trampling, and localized deposition of urine and dung (Glenn et al., 1992; Howison et al., 2017).

Contrary to our hypothesis, the interaction of nutrient addition and herbivore exclusion only had weak positive effects on gamma stability, explained by their joint positive effects on spatial asynchrony (Figure 1). Without nutrient addition, herbivore exclusion decreased spatial asynchrony by 11% on average, which may be due to biotic and abiotic homogenization without disturbances from herbivores (Chase, 2010). Under ambient conditions, herbivores may promote vegetation heterogeneity by grazing preferentially in nutritious patches (Adler et al., 2001). However, under nutrient addition, spatial asynchrony was not affected by herbivores. This may be because adding nutrients increase the compensatory growth of palatable plants after being grazed. Our results suggest weak interactive effects of nutrient addition and herbivore exclusion on plant diversity, aboveground biomass, and the stability of aboveground biomass across spatial scales in global grasslands.

Consistent with our hypothesis, we found that community dissimilarity in time and space was mainly attributable to balanced variation, but only temporal balanced variation was negatively related to alpha stability. Conceptually, temporal balanced variation is similar to species asynchrony, both characterizing compensatory dynamics in communities. But in contrast to species asynchrony that usually positively contributes to alpha stability (Hector et al., 2010), temporal balanced variation reduced it. This can be understood from the fact that temporal balanced variation evaluates absolute changes from individual species, whereas species asynchrony evaluates relative change (i.e. changes induced by individual species relative to overall change in a community). The lack of correlation between spatial asynchrony and spatial community dissimilarity may be because spatial asynchrony was not due to asynchronous dynamics over space but over time (in different blocks). However, spatial and temporal community dissimilarity were positively correlated with each other (Figure 2; Collins et al., 2018). Thus, spatial community dissimilarity may still contribute to decreased stability across spatial scales indirectly through its impacts on temporal community dissimilarity.

Unsurprisingly, variation in climate over time also had strong negative impacts on gamma stability through decreasing alpha stability and spatial asynchrony, confirming that increased extreme climate events threaten ecosystem stability (IPCC, 2019). Moreover, variation in climate may interact with other global change factors such as eutrophication, herbivore loss, fire, and warming to impact plant communities (Collins et al., 2017). Thus, predicting ecosystem stability is getting more challenging as multiple global change factors happening simultaneously has become a defining feature of our world (IPCC, 2019).

Our study fills an important knowledge gap by addressing the effects of the two most significant global change factors in grasslands, eutrophication and herbivore loss, on stability across spatial scales. We found that eutrophication and herbivore loss can simultaneously reduce the temporal stability of biomass production, especially at larger spatial scales. Our results, thus, point to the need to reduce nutrient input while preserving or reintroducing herbivores to ensure stable provisioning of grassland biomass. In particular, reintroducing domestic or wild herbivores to intensively fertilized grasslands may be a good restoration strategy to reduce excessive soil nutrients and increase biodiversity and the stability of biomass production. Our results also highlight that maintaining grassland stability in the face of eutrophication and herbivore loss requires a multiscale framework to disentangle the influences of processes operating at different scales to guide conservation and management practices.

## ACKNOWLEDGMENTS

This work was supported by the National Natural Science Foundation of China (31988102, 32122053). This work was generated using data from the NutNet (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 and NSF-DEB-1831944 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. Nitrogen fertilizer was donated to the NutNet by Crop Production Services, Loveland, CO. We thank Maowei Liang for helpful discussion and two anonymous reviewers and the editors for their constructive comments and suggestions to improve our manuscript.

## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## AUTHOR CONTRIBUTIONS

QC, SW, and YH developed and framed research questions. QC analyzed the data with help from SW and YH. QC wrote the paper with contributions and input from all authors. EWS and ETB are NutNet coordinators. The author contribution matrix is provided in Tables S6 and S7.

## DATA AVAILABILITY STATEMENT

Data associated with this manuscript are publicly available at Figshare: https://doi.org/10.6084/m9.figshare.18278129

## ORCID

*Qingqing Chen* https://orcid.org/0000-0003-1957-3848
*Eric W. Seabloom* https://orcid.org/0000-0001-6780-9259
*Anu Eskelinen* https://orcid.org/0000-0003-1707-5263
*Risto Virtanen* https://orcid.org/0000-0002-8295-8217
*Anita C. Risch* https://orcid.org/0000-0003-0531-8336

## REFERENCES

Adler, P., Raff, D., & Lauenroth, W. (2001). The effect of grazing on the spatial heterogeneity of vegetation. *Oecologia*, *128*, 465–479. https://doi.org/10.1007/s004420100737

Alberti, J., Bakker, E. S., van Klink, R., Olff, H., & Smit, C. (2017). Herbivore exclusion promotes a more stochastic plant community assembly in

a natural grassland. *Ecology*, *98*, 961–970. https://doi.org/10.1002/ecy.1741

Alberti, J., Canepuccia, A., Pascual, J., Pérez, C., & Iribame, O. (2011). Joint control by rodent herbivory and nutrient availability of plant diversity in a salt marsh-salty steppe transition zone. *Journal of Vegetation Science*, *22*, 216–224. https://doi.org/10.1111/j.1654-1103.2010.01240.x

Alberti, J., Méndez Casariego, A., Daleo, P., Fanjul, E., Silliman, B., Bertness, M., & Iribarne, O. (2010). Abiotic stress mediates top-down and bottom-up control in a Southwestern Atlantic salt marsh. *Oecologia*, *163*, 181–191. https://doi.org/10.1007/s00442-009-1504-9

Allan, E., Weisser, W., Weigelt, A., Roscher, C., Fischer, M., & Hillebrand, H. (2011). More diverse plant communities have higher functioning over time due to turnover in complementary dominant species. *Proceedings of the National Academy of Sciences of the United States of America*, *108*, 17034–17039. https://doi.org/10.1073/pnas.1104015108

Anderson, M. J., & Walsh, D. C. I. (2013). PERMANOVA, ANOSIM, and the Mantel test in the face of heterogeneous dispersions: What null hypothesis are you testing? *Ecological Monographs*, *83*, 557–574.

Atwood, T. B., Valentine, S. A., Hammill, E., McCauley, D. J., Madin, E. M. P., Beard, K. H., & Pearse, W. D. (2020). Herbivores at the highest risk of extinction among mammals, birds, and reptiles. *Science Advances*, *6*, abb8458.

Bakker, E. S., Ritchie, M. E., Olff, H., Milchunas, D. G., & Knops, J. M. H. H. (2006). Herbivore impact on grassland plant diversity depends on habitat productivity and herbivore size. *Ecology Letters*, *9*, 780–788. https://doi.org/10.1111/j.1461-0248.2006.00925.x

Baselga, A. (2017). Partitioning abundance-based multiple-site dissimilarity into components: Balanced variation in abundance and abundance gradients. *Methods in Ecology and Evolution*, *8*, 799–808. https://doi.org/10.1111/2041-210X.12693

Baselga, A., & Orme, C. D. L. (2012). Betapart: An R package for the study of beta diversity. *Methods in Ecology and Evolution*, *3*, 808–812.

Beck, J. J., Hernández, D. L., Pasari, J. R., & Zavaleta, E. S. (2015). Grazing maintains native plant diversity and promotes community stability in an annual grassland. *Ecological Applications*, *25*, 1259–1270. https://doi.org/10.1890/14-1093.1

Blüthgen, N., Simons, N. K., Jung, K., Prati, D., Renner, S. C., Boch, S., Fischer, M., Hölzel, N., Klaus, V. H., Kleinebecker, T., Tschapka, M., Weisser, W. W., & Gossner, M. M. (2016). Land use imperils plant and animal community stability through changes in asynchrony rather than diversity. *Nature Communications*, *7*, 1–7. https://doi.org/10.1038/ncomms10697

Borer, E. T., Harpole, W. S., Adler, P. B., Arnillas, C. A., Bugalho, M. N., Cadotte, M. W., Caldeira, M. C., Campana, S., Dickman, C. R., Dickson, T. L., Donohue, I., Eskelinen, A., Firn, J. L., Graff, P., Gruner, D. S., Heckman, R. W., Koltz, A. M., Komatsu, K. J., Lannes, L. S., … Seabloom, E. W. (2020). Nutrients cause grassland biomass to outpace herbivory. *Nature Communications*, *11*, 1–8. https://doi.org/10.1038/s41467-020-19870-y

Borer, E. T., Seabloom, E. W., Gruner, D. S., Harpole, W. S., Hillebrand, H., Lind, E. M., Adler, P. B., Alberti, J., Anderson, T. M., Bakker, J. D., Biederman, L., Blumenthal, D., Brown, C. S., Brudvig, L. A., Buckley, Y. M., Cadotte, M., Chu, C., Cleland, E. E., Crawley, M. J., … Yang, L. H. (2014a). Herbivores and nutrients control grassland plant diversity via light limitation. *Nature*, *508*, 517–520. https://doi.org/10.1038/nature13144

Borer, E. T., Seabloom, E. W., Gruner, D. S., Harpole, W. S., Hillebrand, H., Lind, E. M., Adler, P. B., Alberti, J., Anderson, T. M., Bakker, J. D., Biederman, L., Blumenthal, D., Brown, C. S., Brudvig, L. A., Buckley, Y. M., Cadotte, M., Chu, C., Cleland, E. E., Crawley, M. J., … Yang, L. H. (2014b). Herbivores and nutrients control grassland plant diversity via light limitation. *Nature*, *508*, 517–520. https://doi.org/10.1038/nature13144

Chase, J. M. (2010). Stochastic community assembly causes higher biodiversity in more productive environments. *Science*, *328*, 1388–1391. https://doi.org/10.1126/science.1187820

Chase, J. M., Leibold, M. A., Downing, A. L., & Shurin, J. B. (2000). The effects of productivity, herbivory, and plant species turnover in grassland food webs. *Ecology*, *81*, 2485. https://doi.org/10.1890/0012-9658(2000)081[2485:TEOPHA]2.0.CO;2

Chen, Q., Bakker, J. P., Alberti, J., Bakker, E. S., Smit, C., & Olff, H. (2021). Long-term cross-scale comparison of grazing and mowing on plant diversity and community composition in a salt-marsh system. *Journal of Ecology*, *109*, 3737–3747. https://doi.org/10.1111/1365-2745.13753

Chen, Q., Howison, R. A., Bakker, J. P., Alberti, J., Kuijper, D. P. J., Olff, H., & Smit, C. (2019). Small herbivores slow down species loss up to 22 years but only at early successional stage. *Journal of Ecology*, *107*, 2688–2696. https://doi.org/10.1111/1365-2745.13236

Collins, S. L., Avolio, M. L., Gries, C., Hallett, L. M., Koerner, S. E., La Pierre, K. J., Rypel, A. L., Sokol, E. R., Fey, S. B., Flynn, D. F. B., Jones, S. K., Ladwig, L. M., Ripplinger, J., & Jones, M. B. (2018). Temporal heterogeneity increases with spatial heterogeneity in ecological communities. *Ecology*, *99*, 858–865. https://doi.org/10.1002/ecy.2154

Collins, S. L., Ladwig, L. M., Petrie, M. D., Jones, S. K., Mulhouse, J. M., Thibault, J. R., & Pockman, W. T. (2017). Press–pulse interactions: Effects of warming, N deposition, altered winter precipitation, and fire on desert grassland community structure and dynamics. *Global Change Biology*, *23*, 1095–1108.

Craven, D., Eisenhauer, N., Pearse, W. D., Hautier, Y., Isbell, F., Roscher, C., Bahn, M., Beierkuhnlein, C., Bönisch, G., Buchmann, N., Byun, C., Catford, J. A., Cerabolini, B. E. L., Cornelissen, J. H. C., Craine, J. M., De Luca, E., Ebeling, A., Griffin, J. N., Hector, A., … Manning, P. (2018). Multiple facets of biodiversity drive the diversity – stability relationship. *Nature Ecology & Evolution*, *2*, 1579–1587. https://doi.org/10.1038/s41559-018-0647-7

Donohue, I., Petchey, O. L., Montoya, J. M., Jackson, A. L., McNally, L., Viana, M., Healy, K., Lurgi, M., O'Connor, N. E., & Emmerson, M. C. (2013). On the dimensionality of ecological stability. *Ecology Letters*, *16*, 421–429. https://doi.org/10.1111/ele.12086

Endara, M. J., & Coley, P. D. (2011). The resource availability hypothesis revisited: A meta-analysis. *Functional Ecology*, *25*, 389–398. https://doi.org/10.1111/j.1365-2435.2010.01803.x

Galloway, J. N., Dentener, F. J., Capone, D. G., Boyer, E. W., Howarth, R. W., Seitzinger, S. P., Asner, G. P., Cleveland, C. C., Green, P. A., Holland, E. A., Karl, D. M., Michaels, A. F., Porter, J. H., Townsend, A. R., & Vösmarty, C. J. (2004). Nitrogen cycles: Past, present, and future. *Biogeochemistry*, *70*(2), 153–226. https://doi.org/10.1007/s10533-004-0370-0

Ganjurjav, H., Zhang, Y., Gornish, E. S., Hu, G., Li, Y., Wan, Y., & Gao, Q. (2019). Differential resistance and resilience of functional groups to livestock grazing maintain ecosystem stability in an alpine steppe on the Qinghai-Tibetan Plateau. *Journal of Environmental Management*, *251*, 109579. https://doi.org/10.1016/j.jenvman.2019.109579

García-Palacios, P., Gross, N., Gaitán, J., & Maestre, F. T. (2018). Climate mediates the biodiversity–ecosystem stability relationship globally. *Proceedings of the National Academy of Sciences of the United States of America*, *115*, 8400–8405. https://doi.org/10.1073/pnas.1800425115

Gilbert, B., MacDougall, A. S., Kadoya, T., Akasaka, M., Bennett, J. R., Lind, E. M., Flores-Moreno, H., Firn, J., Hautier, Y., Borer, E. T., Seabloom, E. W., Adler, P. B., Cleland, E. E., Grace, J. B., Harpole, W. S., Esch, E. H., Moore, J. L., Knops, J., McCulley, R., … Fay, P. A. (2020). Climate and local environment structure asynchrony and the stability of primary production in grasslands. *Global Ecology and Biogeography*, *29*, 1177–1188. https://doi.org/10.1111/geb.13094

Glenn, S. M., Collins, S. L., & Gibson, D. J. (1992). Disturbances in tallgrass prairie: Local and regional effects on community heterogeneity.

*Landscape Ecology*, *7*, 243–251. https://doi.org/10.1007/BF00131255

Gonzalez, A., & Loreau, M. (2009). The causes and consequences of compensatory dynamics in ecological communities. *Annual Review of Ecology Evolution and Systematics*, *40*, 393–414. https://doi.org/10.1146/annurev.ecolsys.39.110707.173349

Grellmann, D. (2002). Plant responses to fertilization and exclusion of grazers on an arctic tundra heath. *Oikos*, *98*, 190–204. https://doi.org/10.1034/j.1600-0706.2002.980202.x

Grime, J. P. (1998). Benefits of plant diversity to ecosystems: Immediate, filter and founder effects. *Journal of Ecology*, *86*, 902–910. https://doi.org/10.1046/j.1365-2745.1998.00306.x

Grman, E., Lau, J. A., Schoolmaster, D. R., & Gross, K. L. (2010). Mechanisms contributing to stability in ecosystem function depend on the environmental context. *Ecology Letters*, *13*, 1400–1410. https://doi.org/10.1111/j.1461-0248.2010.01533.x

Halpern, B. S., Borer, E. T., Seabloom, E. W., & Shurin, J. B. (2005). Predator effects on herbivore and plant stability. *Ecology Letters*, *8*, 189–194. https://doi.org/10.1111/j.1461-0248.2004.00712.x

Hartley, S. E., & Mitchell, R. J. (2005). Manipulation of nutrients and grazing levels on heather moorland: Changes in Calluna dominance and consequences for community composition. *Journal of Ecology*, *93*, 990–1004. https://doi.org/10.1111/j.1365-2745.2005.01025.x

Hautier, Y., Tilman, D., Isbell, F., Seabloom, E. W., Borer, E. T., & Reich, P. B. (2015). Supplementary for Anthropogenic environmental changes affect ecosystem stability via biodiversity. *Science*, *348*, 336–340. https://doi.org/10.1126/science.aaa1788

Hautier, Y., Zhang, P., Loreau, M., Wilcox, K. R., Seabloom, E. W., Borer, E. T., Byrnes, J. E. K., Koerner, S. E., Komatsu, K. J., Lefcheck, J. S., Hector, A., Adler, P. B., Alberti, J., Arnillas, C. A., Bakker, J. D., Brudvig, L. A., Bugalho, M. N., Cadotte, M., Caldeira, M. C., … Wang, S. (2020). General destabilizing effects of eutrophication on grassland productivity at multiple spatial scales. *Nature Communications*, *11*, 1–9. https://doi.org/10.1038/s41467-020-19252-4

Hector, A., Hautier, Y., Saner, P., Wacker, L., Bagchi, R., Joshi, J., Scherer-Lorenzen, M., Spehn, E. M., Bazeley-White, E., Weilenmann, M., Caldeira, M. C., Dimitrakopoulos, P. G., Finn, J. A., Huss-Danell, K., Jumpponen, A., Mulder, C. P. H., Palmborg, C., Pereira, J. S., Siamantziouras, A. S. D., … Loreau, M. (2010). General stabilizing effects of plant diversity on grassland productivity through population asynchrony and overyielding. *Ecology*, *91*, 2213–2220. https://doi.org/10.1890/09-1162.1

Hillebrand, H., Gruner, D. S., Borer, E. T., Bracken, M. E. S., Cleland, E. E., Elser, J. J., Harpole, W. S., Ngai, J. T., Seabloom, E. W., Shurin, J. B., & Smith, J. E. (2007). Consumer versus resource control of producer diversity depends on ecosystem type and producer community structure. *Proceedings of the National Academy of Sciences of the United States of America*, *104*, 10904–10909. https://doi.org/10.1073/pnas.0701918104

Hillebrand, H., & Kunze, C. (2020). Meta-analysis on pulse disturbances reveals differences in functional and compositional recovery across ecosystems. *Ecology Letters*, *23*, 575–585. https://doi.org/10.1111/ele.13457

Hodapp, D., Borer, E. T., Harpole, W. S., Lind, E. M., Seabloom, E. W., Adler, P. B., Alberti, J., Arnillas, C. A., Bakker, J. D., Biederman, L., Cadotte, M., Cleland, E. E., Collins, S., Fay, P. A., Firn, J., Hagenah, N., Hautier, Y., Iribarne, O., Knops, J. M. H., … Hillebrand, H. (2018). Spatial heterogeneity in species composition constrains plant community responses to herbivory and fertilisation. *Ecology Letters*, *21*, 1364–1371. https://doi.org/10.1111/ele.13102

Howison, R. A., Olff, H., Van De Koppel, J., & Smit, C. (2017). Biotically driven vegetation mosaics in grazing ecosystems: The battle between bioturbation and biocompaction. *Ecological Monographs*, *87*, 363–378. https://doi.org/10.1002/ecm.1259

IPCC. (2019). Summary for policymakers. In P. R. Shukla, J. Skea, E. Calvo Buendia, V. Masson-Delmotte, H.-O. Pörtner, D. C. Roberts, P. Zhai, R. Slade, S. Connors, R. van Diemen, M. Ferrat, E. Haughey, S. Luz, S. Neogi, M. Pathak, J. Petzold, J. Portugal Pereira, P. Vyas, E. Huntley, K. Kissick, M. Belkacemi, & J. Malley (Eds.), *Climate change and land: An IPCC special report on climate change, desertification, land degradation, sustainable land management, food security, and greenhouse gas fluxes in terrestrial ecosystems* (p. 5). World Meterological Organization.

Isbell, F., Gonzalez, A., Loreau, M., Cowles, J., Díaz, S., Hector, A., Mace, G. M., Wardle, D. A., O'Connor, M. I., Duffy, J. E., Turnbull, L. A., Thompson, P. L., & Larigauderie, A. (2017). Linking the influence and dependence of people on biodiversity across scales. *Nature*, *546*, 65–72. https://doi.org/10.1038/nature22899

Koerner, S. E., Avolio, M. L., La Pierre, K. J., Wilcox, K. R., Smith, M. D., & Collins, S. L. (2016). Nutrient additions cause divergence of tallgrass prairie plant communities resulting in loss of ecosystem stability. *Journal of Ecology*, *104*, 1478–1487. https://doi.org/10.1111/1365-2745.12610

Koerner, S. E., Smith, M. D., Burkepile, D. E., Hanan, N. P., Avolio, M. L., Collins, S. L., Knapp, A. K., Lemoine, N. P., Forrestel, E. J., Eby, S., Thompson, D. I., Aguado-Santacruz, G. A., Anderson, J. P., Anderson, T. M., Angassa, A., Bagchi, S., Bakker, E. S., Bastin, G., Baur, L. E., … Zelikova, T. J. (2018). Change in dominance determines herbivore effects on plant biodiversity. *Nature Ecology & Evolution*, *2*, 1925–1932. https://doi.org/10.1038/s41559-018-0696-y

Lamy, T., Wisnoski, N. I., Andrade, R., Castorani, M. C. N., Compagnoni, A., Lany, N., Marazzi, L., Record, S., Swan, C. M., Tonkin, J. D., Voelker, N., Wang, S., Zarnetske, P. L., & Sokol, E. R. (2021). The dual nature of metacommunity variability. *Oikos*, *130*(12), 2078–2092. https://doi.org/10.1111/oik.08517

Lefcheck, J. S. (2016). piecewiseSEM: Piecewise structural equation modelling in r for ecology, evolution, and systematics. *Methods in Ecology and Evolution*, *7*, 573–579.

Liang, M., Liang, C., Hautier, Y., Wilcox, K. R., & Wang, S. (2021). Grazing-induced biodiversity loss impairs grassland ecosystem stability at multiple scales. *Ecology Letters*, *24*, 2054–2064. https://doi.org/10.1111/ele.13826

Liu, J., Li, X., Ma, Q., Zhang, X., Chen, Y., Isbell, F., & Wang, D. (2019). Nitrogen addition reduced ecosystem stability regardless of its impacts on plant diversity. *Journal of Ecology*, *107*, 2427–2435. https://doi.org/10.1111/1365-2745.13187

Liu, J., Yang, X., Ghanizadeh, H., Guo, Q., Fan, Y., Zhang, B., Yan, X., Wen, Z., & Li, W. (2021). Long-term enclosure can benefit grassland community stability on the loess plateau of China. *Sustainability*, *13*, 1–19.

Macdougall, A. S., McCann, K. S., Gellner, G., & Turkington, R. (2013). Diversity loss with persistent human disturbance increases vulnerability to ecosystem collapse. *Nature*, *494*, 86–89. https://doi.org/10.1038/nature11869

Milchunas, D. G., & Lauenroth, W. W. (1993). Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecological Monographs*, *63*, 327–366. https://doi.org/10.2307/2937150

Molina, C. D., Tognetti, P. M., Graff, P., & Chaneton, E. J. (2021). Mowing does not redress the negative effect of nutrient addition on alpha and beta diversity in a temperate grassland. *Journal of Ecology*, *109*, 1501–1510. https://doi.org/10.1111/1365-2745.13573

Moran, M. D., & Scheidler, A. R. (2002). Effects of nutrients and predators on an old-field food chain: Interactions of top-down and bottom-up processes. *Oikos*, *98*, 116–124. https://doi.org/10.1034/j.1600-0706.2002.980112.x

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & R Core Team. (2017). nlme: Linear and nonlinear mixed effects models. R Package version 3.1-131.

Polley, H. W., Wilsey, B. J., & Derner, J. D. (2007). Dominant species constrain effects of species diversity on temporal variability in biomass production of tallgrass prairie. *Oikos*, *116*, 2044–2052. https://doi.org/10.1111/j.2007.0030-1299.16080.x

Proulx, M., & Mazumder, A. (1998). Reversal of grazing impact on plant species richness in nutrient-poor vs. nutrient-rich ecosystems. *Ecology*, *79*, 2581–2592.

Qin, J., Ren, H., Han, G., Zhang, J., Browning, D., Willms, W., & Yang, D. (2019). Grazing reduces the temporal stability of temperate grasslands in northern China. *Flora*, *259*, 151450. https://doi.org/10.1016/j.flora.2019.151450

R Core Team. (2020). *R: A language and environment for statistical computing*. Foundation for Statistical Computing.

Ren, H., Taube, F., Stein, C., Zhang, Y., Bai, Y., & Hu, S. (2018). Grazing weakens temporal stabilizing effects of diversity in the Eurasian steppe. *Ecology and Evolution*, *8*, 231–241. https://doi.org/10.1002/ece3.3669

Ripple, W. J., Wolf, C., Newsome, T. M., Betts, M. G., Ceballos, G., Courchamp, F., Hayward, M. W., Valkenburgh, B., Wallach, A. D., & Worm B. (2019). Are we eating the world's megafauna to extinction? *Conservation Letters*, *12*, e12627.

Saruul, K., Jiangwen, L. I., Jianming, N., Qing, Z., Xuefeng, Z., Guodong, H., Mengli, Z., & Haifeng, B. (2019). Typical steppe ecosystems maintain high stability by decreasing the connections among recovery, resistance, and variability under high grazing pressure. *Science of the Total Environment*, *659*, 1146–1157. https://doi.org/10.1016/j.scitotenv.2018.12.447

Seabloom, E. W., Borer, E. T., Buckley, Y., Cleland, E. E., Davies, K., Firn, J., Harpole, W. S., Hautier, Y., Lind, E., MacDougall, A., Orrock, J. L., Prober, S. M., Adler, P., Alberti, J., Michael Anderson, T., Bakker, J. D., Biederman, L. A., Blumenthal, D., Brown, C. S., … Yang, L. (2013). Predicting invasion in grassland ecosystems: Is exotic dominance the real embarrassment of richness? *Global Change Biology*, *19*, 3677–3687.

Shannon, C. E. (1948). A mathematical theory of communication. *Bell System Technical Journal*, *27*, 623–656. https://doi.org/10.1002/j.1538-7305.1948.tb00917.x

Tilman, D. (1987). Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. *Ecological Monographs*, *57*, 190–214. https://doi.org/10.2307/2937080

Tilman, D., Fargione, J., Wolff, B., D'Antonio, C., Dobson, A., Howarth, R., Schindler, D., Schlesinger, W. H., Simberloff, D., & Swackhamer D. (2001). Forecasting agriculturally driven global environmental change. *Science*, *292*, 281–284.

Tilman, D., Reich, P. B., & Knops, J. M. H. (2006). Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature*, *441*, 629–632.

Wang, S., Lamy, T., Hallett, L. M., & Loreau, M. (2019). Stability and synchrony across ecological hierarchies in heterogeneous metacommunities: Linking theory to data. *Ecography*, *42*, 1200–1211. https://doi.org/10.1111/ecog.04290

Wang, S., & Loreau, M. (2016). Biodiversity and ecosystem stability across scales in metacommunities. *Ecology Letters*, *19*, 510–518. https://doi.org/10.1111/ele.12582

Wang, S., Loreau, M., Mazancourt, C., Isbell, F., Beierkuhnlein, C., Connolly, J., Deutschman, D. H., Doležal, J., Eisenhauer, N., Hector, A., Jentsch, A., Kreyling, J., Lanta, V., Lepš, J., Polley, H. W., Reich, P. B., Ruijven, J., Schmid, B., Tilman, D., … Craven, D. (2021). Biotic homogenization destabilizes ecosystem functioning by decreasing spatial asynchrony. *Ecology*, *102*, 1–10. https://doi.org/10.1002/ecy.3332

Whittaker, R. H. (1972). Evolution and measurement of species diversity. *Taxon*, *21*, 213–251.

White, L., O'Connor, N. E., Yang, Q., Emmerson, M. C., & Donohue, I. (2020). Individual species provide multifaceted contributions to the stability of ecosystems. *Nature Ecology & Evolution*, *4*, 1594–1601. https://doi.org/10.1038/s41559-020-01315-w

Wilcox, K. R., Tredennick, A. T., Koerner, S. E., Grman, E., Hallett, L. M., Avolio, M. L., La Pierre, K. J., Houseman, G. R., Isbell, F., Johnson, D. S., Alatalo, J. M., Baldwin, A. H., Bork, E. W., Boughton, E. H., Bowman, W. D., Britton, A. J., Cahill, J. F., Collins, S. L., Du, G., … Zhang, Y. (2017). Asynchrony among local communities stabilises ecosystem function of metacommunities. *Ecology Letters*, *20*, 1534–1545. https://doi.org/10.1111/ele.12861

Winfree, R., Fox, J. W., Williams, N. M., Reilly, J. R., & Cariveau, D. P. (2015). Abundance of common species, not species richness, drives delivery of a real-world ecosystem service. *Ecology Letters*, *18*, 626–635. https://doi.org/10.1111/ele.12424

Worm, B., Lotze, H. K., Hillebrand, H., & Sommer, U. (2002). Consumer versus resource control of species diversity and ecosystem functioning. *Nature*, *417*, 848–851. https://doi.org/10.1038/nature00830

Yang, Z., Guo, H., Zhang, J., & Du, G. (2013). Stochastic and deterministic processes together determine alpine meadow plant community composition on the Tibetan Plateau. *Oecologia*, *171*, 495–504. https://doi.org/10.1007/s00442-012-2433-6

Zelikova, T. J., Blumenthal, D. M., Williams, D. G., Souza, L., LeCain, D. R., Morgan, J., & Pendall, E. (2014). Long-term exposure to elevated $CO_2$ enhances plant community stability by suppressing dominant plant species in a mixed-grass prairie. *Proceedings of the National Academy of Sciences of the United States of America*, *111*, 15456–15461. https://doi.org/10.1073/pnas.1414659111

Zhang, Y., Feng, J., Loreau, M., He, N., Han, X., & Jiang, L. (2019). Nitrogen addition does not reduce the role of spatial asynchrony in stabilising grassland communities. *Ecology Letters*, *22*, 563–571. https://doi.org/10.1111/ele.13212

## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

**How to cite this article:** Chen, Q., Wang, S., Seabloom, E. W., MacDougall, A. S., Borer, E. T., Bakker, J. D., Donohue, I., Knops, J. M. H., Morgan, J. W., Carroll, O., Crawley, M., Bugalho, M. N., Power, S. A., Eskelinen, A., Virtanen, R., Risch, A. C., Schütz, M., Stevens, C., Caldeira, M. C., … Hautier, Y. (2022). Nutrients and herbivores impact grassland stability across spatial scales through different pathways. *Global Change Biology*, 28, 2678–2688. https://doi.org/10.1111/gcb.16086