

Short-term versus multi-decadal responses of community synchrony, biodiversity, and stability to multiple global change drivers

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Abstract

Global change drivers alter multiple components of community composition, with cascading impacts on ecosystem stability. However, few studies have examined the complex interplay between global change drivers, synchrony, and diversity, especially over long-term successional dynamics. We analyzed a 22-year time series of grassland community data from Cedar Creek, USA, to examine the joint effects of pulse soil disturbance and press nitrogen addition on community synchrony, diversity, and stability during transient and post-transient periods of succession. Using multiple regression and structural equation modeling, we found that global change drivers decreased both synchrony and stability, thereby decoupling classic theoretical relationships, such as the portfolio effect. While the effect of soil disturbance weakened through time, nitrogen addition induced unexpected dynamics with maintained long-term impacts on composition, synchrony, and stability. Our findings underscore the need for long-term data and a comprehensive approach when managing ecosystems under ongoing global environmental changes.

Introduction

Global change drivers such as agricultural disturbances, fertilization, atmospheric nutrient deposition, and warming temperatures threaten ecosystems around the world (Pounds *et al.*, 2006; Stevens *et al.*, 2010; Pachauri *et al.*, 2014). Global change drivers alter multiple community assembly processes, ultimately altering the maintenance of species richness and the stability of biomass production (Tilman 1985; Muehleisen *et al.*, 2022), with simultaneous global change drivers yielding strong, interactive effects (Zhu *et al.*, 2016; Collins *et al.*, 2022; Komatsu *et al.*, 2019). While the independent and interactive effects of global change drivers on ecological diversity and stability have been well explored (Tilman, 1985; Komatsu *et al.*, 2019; Avolio *et al.*, 2021), the impact of multiple

interacting drivers on temporal community dynamics are less understood, particularly contrasting observed short-term effects to those observed over long time series (Valencia *et al.*, 2020a; Ebel *et al.*, 2022). Yet, long-term temporal community patterns, such as changes in synchrony (e.g. correlations in temporal fluctuations in species' abundances) or temporal trends in the magnitude and direction of global change drivers, play critical roles in predicting global change effects on ecosystem dynamics.

Global change drivers commonly impact community composition, including diversity and evenness patterns. For example, increased nutrient loading in grassland communities shifts competitive hierarchies by decreasing native biodiversity and increasing invasive species dominance (Stevens *et al.*, 2004; Borer *et al.*, 2017; Tilman, 1985; Seabloom *et al.*, 2020). These changes in dominance and local extinction events are driven by species' direct responses to global change and environmentally-induced changes in species interaction strengths (Collins *et al.*, 2022; Weiss-Lehman *et al.*, 2022). Therefore, shifting community compositions likely result from multiple consequences of global change, including species loss/gain, changes in evenness, and species reordering, which can occur on different timescales (Avolio *et al.*, 2021). Furthermore, shifts in community composition under global change often negatively impact ecosystem stability (Tilman *et al.*, 1996; Hautier *et al.*, 2015); for example, fertilization increased interannual variability of biomass across global grasslands (Carroll *et al.*, 2022).

While previous global change studies have emphasized changes in species abundances and community composition, temporal dynamics such as community synchrony are also impacted by environmental changes. Community synchrony quantifies correlations in temporal fluctuations in species' abundances and strongly depends on species interactions and responses to environmental conditions (Loreau & de Mazancourt, 2013). Highly synchronous dynamics can arise from shared responses to environmental fluctuations, destabilizing aggregate community properties, like total biomass (Tilman & Downing,

1994; Ives *et al.*, 1999; Valencia *et al.*, 2020a). Conversely, compensatory dynamics are the tendency for periods of low abundance of some species to be offset by high abundance in other species and are often driven by strong competition or opposing responses to environmental fluctuations, thereby increasing stability (Ives *et al.*, 1999; Yachi & Loreau, 1999; Loreau & de Mazancourt, 2013). Theory predicts that shifts in dominance and species richness alter temporal stability via changes in synchrony (Doak, 1998; Tilman, 1998). Higher richness increases a community’s portfolio and the likelihood of species responding differently to fluctuating environments, decreasing synchrony and increasing stability. If global change drivers impact portfolio effects, they could have downstream repercussions on synchrony and stability.

Synchrony is influenced by timescale-dependent shifts in composition, lagged community responses, and interactions among multiple global change drivers (Komatsu *et al.*, 2019; Downing *et al.*, 2008; Shoemaker *et al.*, 2022; Sheppard *et al.*, 2016). Timescale-specific correlations among interacting environmental drivers can further affect the magnitude of synchrony (Desharnais *et al.*, 2018), motivating the need to examine the effects of global change on community dynamics using long-term data. It is important to examine these interdependent changes in synchrony, biodiversity, and stability across long time series, as certain drivers, such as pulse disturbances (e.g., drought, fire, or tilling), can co-occur with ongoing press disturbance (e.g., atmospheric nitrogen deposition, warming). For example, long-term experiments show that disturbance may impact community composition (Valencia *et al.*, 2020b; DeSiervo *et al.*, 2023), while interactive effects with other global change drivers could determine long-term competitive dominance and resilience (Komatsu *et al.*, 2019). Studies show conflicting relationships between global change, biodiversity, and synchrony, including weakly decreased synchrony across a meta-analysis of multiple treatments (Valencia *et al.*, 2020a), decreased synchrony with climate variability (Gilbert *et al.*, 2020), increased synchrony with drought (Ebel *et al.*, 2022), and changes in community richness, evenness, and

synchrony mediating global change effects on stability (Gu *et al.*, 2023). These conflicting results may stem from differences in the timespans of studies, as community relationships shift through time and new effects appear late in succession.

Understanding synchrony and stability in grasslands is crucial due to their significant roles in food supply (O'Mara, 2012), carbon sequestration (Soussana *et al.*, 2004), and other ecosystem services (Bengtsson *et al.*, 2019). Temperate grasslands face extensive land-use alterations (Mock, 2000; Newbold *et al.*, 2016), while contending with widespread nutrient increases from agricultural runoff and atmospheric nitrogen deposition (Gruber & Galloway, 2008). Here, we examine how multiple global change drivers—nitrogen addition coupled with soil disturbance—impact grassland community synchrony, stability, and diversity across successional timescales. We use data from a 22-year fully factorial grassland experiment at the Cedar Creek Ecosystem Reserve in Minnesota, USA. We build on previous work from Cedar Creek showing changes in species richness and community composition under disturbance and nitrogen addition (Seabloom *et al.*, 2020), and that the system recovered to novel, nutrient-mediated equilibria after approximately a decade of transient dynamics (DeSiervo *et al.*, 2023). We ask: (1) How do disturbance and nitrogen addition alter community synchrony? (2) To what extent do community properties of richness, evenness, and synchrony jointly alter community stability with multiple global change drivers? and (3) How do these relationships change through succession? We hypothesized that disturbance would increase community synchrony (Table S1, H6), but nitrogen addition may increase or decrease synchrony (Table S1, H2), dependent on changes in species interactions. Nitrogen addition and soil disturbance were expected to decrease stability (Table S1, H1, H5) by increasing biomass in favorable years of growth (Lee *et al.*, 2010), leading to larger synchronized booms and busts in species biomass. We also expected decreased richness due to nitrogen addition and disturbance (Seabloom *et al.*, 2020) would decrease stability due to portfolio loss (Lehman & Tilman, 2000; Loreau *et al.*,

2021; Doak 1998).

Materials and Methods

Study Site and Data Collection

We used annual above-ground biomass data collected for 22 years (1982 - 2004) from long-term grassland experiments at the Cedar Creek Ecosystem Science Reserve in Minnesota, USA. The system has sandy soils naturally deficient in nitrogen (N). Mean annual temperature averaged across the 22 years was 6.7°C (\pm 0.02 SE), and mean annual precipitation was 818 mm (\pm 35 SE).

We briefly describe the experiment, with additional details in Tilman (1987) and Seabloom *et al.* (2020). In 1982, identical nutrient addition experiments were established within two grids (35 x 55 m), replicated in three agricultural fields that were abandoned in 1968 (Field A), 1957 (Field B), and 1934 (Field C). Old field vegetation was left intact in one grid within each field (E001) (Tilman, 2021b), while the other grid was disked to disturb the soil and restart succession in the spring of 1982 (E002) (Tilman, 2021a). Each grid was split into 54 vegetation plots (4 X 4 m) for a total of 324 plots. Six replicate plots within each grid received one of nine nutrient addition treatments annually. Nutrient addition treatments included a control (no nutrient addition), micronutrients (μ) only, and seven levels of nitrogen addition plus μ : 1.0, 3.4, 5.4, 9.5, 17.0, and 27.2 g N \cdot m² \cdot year⁻¹. Nitrogen was added annually as NH₄NO₃, and micronutrients (μ) consisted of P, K, Ca, Mg, S, and citrate-chelated trace metals (see Supplementary Methods for detailed micronutrient amounts). We used the 0 g N + μ \cdot m² \cdot year⁻¹ as our control for analyses to hold the addition of micronutrients constant (see Supplementary Methods, Comparison of Control Conditions).

Above-ground biomass was clipped annually in a 10 x 300 cm strip, sorted to species,

dried, and weighed to the nearest 0.01 g. All plots were sampled annually from 1982 to 2004, except for 1995 (only E001 sampled), 2001 (only E001 sampled), and 2003 (only E001 and Field C in E002 sampled). From 1992 onwards, three plots were randomly assigned to different nutrient cessation or burning treatments in each field. These plots were omitted from our analyses, resulting in 216 total. We analyzed species level and aggregated community biomass, removing woody species except for low-lying shrubs (see Supplementary Methods, Data Cleaning). Finally, we visualized annual time series data for the most abundant species of six functional groups (C4 grasses, C3 grasses, annual and perennial non-leguminous forbs, legumes, and low-lying shrubs) in intact and disturbed treatments under control ($0 \text{ g N} \cdot \text{m}^2 \cdot \text{year}^{-1}$) and $9.5 \text{ g N} \cdot \text{m}^2 \cdot \text{year}^{-1}$ conditions to understand temporal trends in biomass.

Long-Term Time Series Analyses

We investigated how synchrony, stability, and their relationship depended on nitrogen addition and soil disturbance across the full 22-year time series. We quantified community synchrony using the classic variance ratio (VR), which compares community-level temporal variance (numerator) to the sum of individual population variances (denominator) (Schluter, 1984; Houlihan *et al.*, 2007; Hallett *et al.*, 2014; Loreau & de Mazancourt, 2008).

The variance ratio is determined as:

$$VR = \frac{\text{var}(C(t))}{\sum_{i=1}^N \text{var}(P_i(t))} \quad (1)$$

Where $P_i(t)$ is the above-ground biomass of species $i = 1, \dots, N$, and the variance is calculated over time $t = 1, \dots, T$. The temporal variance of the aggregate community biomass, $\text{var}(C(t))$ is further calculated as:

$$\text{var}(C(t)) = \sum_{i=1}^N \text{var}(P_i(t)) + 2 \sum_{i=1}^{N-1} \sum_{j=i+1}^N \text{cov}(P_i(t), P_j(t)).$$

Thus, the covariances move the ratio away from 1, where a variance ratio greater than 1 indicates synchronous dynamics, or positive species covariance on average over the pairwise species comparisons, and a variance ratio less than 1 indicates compensatory dynamics, or negative species covariance on average.

We quantified ecosystem stability as the inverse coefficient of variation (Tilman, 1999):

$$CV^{-1} = \frac{\mu}{\sigma} \quad (2)$$

where μ represents the mean annual biomass of the community, and σ represents the temporal standard deviation of community biomass. Synchrony and stability were calculated using the `codyn` package (Hallett *et al.* 2016), and all statistical analyses were conducted in R version 4.3.1 (R Core Team, 2020).

To investigate the joint effects of nutrient addition and soil disturbance on synchrony and stability, we fit multiple regression models for each response variable (synchrony, stability), including an interaction effect between nitrogen addition (continuous) and disturbance (categorical). We included field (categorical) as a fixed effect and grid (categorical) as a random effect in all models. We compared linear versus quadratic fits across the nitrogen gradient for synchrony and stability models to account for potential non-linear relationships. We determined the best model fit using the Akaike Information Criterion (AIC).

To better understand global change effects on synchrony and stability, we decomposed the variance ratio (Eqn. 1) and inverse coefficient of variation (Eqn. 2) into their components. For synchrony, we compared how treatments affected changes in community variability, $\text{var}(C(t))$, to changes in aggregate population variability, $\sum_i^N \text{var}(P_i(t))$. For stability, we examined whether treatments had a larger effect on the temporal variability of biomass (σ) or mean biomass (μ) (Carroll *et al.* 2022). We estimated how nitrogen

addition and soil disturbance influenced each component metric, using multiple regression to assess the effect of nitrogen addition, disturbance, and their interaction, modeling field as a fixed effect and grid as a random effect (following the split-plot design with a randomized complete block design at the whole-plot level).

Successional Dynamics

To determine the effect of global change drivers during transient early successional versus post-transient dynamical-equilibria periods, we subdivided our time series into a transient period that included data from 1982 to 1988 and a post-transient period using 1993 to 2004 data. We chose time windows encompassing seven years of data to facilitate cross-period comparison while having long enough time series to obtain stable estimates of synchrony and stability (e.g. [Hallett *et al.* 2014](#), [Zhao *et al.* 2020](#), [Walter *et al.* 2021](#)). We removed 1989 - 1992 to omit the compositional transition from succession to dynamical equilibria, based on results from DeSiervo *et al.* ([2023](#)). Results are robust to different time series windows (e.g., 7 versus 10-year). We fitted separate linear models within each combination of nitrogen, disturbance treatment, and successional period to visualize variation in the synchrony-stability relationship in the transient versus post-transient phases.

Community composition and species diversity also influence stability ([Tilman 1987](#)), motivating us to examine direct and indirect pathways from soil disturbance and nitrogen addition to biodiversity, synchrony, and stability using structural equation models (SEM). We incorporated species richness and evenness as biodiversity metrics. We calculated species richness by determining the maximum number of species censused annually in each plot and averaging these per-plot richnesses across the years in transient and post-transient phases. We evaluated species evenness using the E_{var} metric ([Smith & Wilson 1996](#)), which computes the variance in log-abundances of all species, then transforms to a standard scale between 0

196 and 1:

$$E_{var} = 1 - \frac{2}{\pi} \arctan(\hat{\sigma}_{\ln(x)}^2) \quad (3)$$

197 where $\hat{\sigma}_{\ln(x)}^2$ is $(n - 1)/n$ times the sample variance of log-abundances of species in a given
198 community. We opted to use this E_{var} metric in favor of the more common Pielou’s evenness
199 index (Pielou, 1966) as Pielou’s index incorporates species richness in the calculation, thus
200 resulting in a mathematically-driven relationship between the two metrics, whereas E_{var} is
201 independent of richness (Smith & Wilson, 1996).

202 We constructed a SEM for each successional period to examine multidimensional
203 community relationships and compare how the strength of pathways changed during
204 succession. Each endogenous variable was examined for normality, and we applied Box-Cox
205 transformations to non-normal data. All continuous variables were standardized to mean 0
206 and unit variance. For each period, we evaluated each pathway’s strength and sign using
207 standardized path coefficients, which represent hypothesized causal relationships. Each
208 SEM included a direct pathway from the two exogenous factors of soil disturbance and
209 nitrogen addition to species richness, evenness, synchrony, and stability. We also included
210 pathways from species richness and evenness to synchrony and stability and from species
211 richness to evenness. Each pathway relationship was justified with a hypothesis (Table S1).
212 The SEMs were fully saturated with all possible pathways (paralleling methods from
213 Figueredo 2013; Jenkins *et al.* 2021); as such, fit statistics are not meaningful for these
214 exploratory models. Instead, we focused our analyses on path comparisons and did not
215 eliminate pathways based on null hypothesis tests, as a comparison between the transient
216 and post-transient phases requires the same model structure. We examined two additional
217 SEMs where we decomposed synchrony and stability into their components (see
218 Supplementary Methods). All SEM models were fitted using the `piecewiseSEM` (Lefcheck,
219 2016) and `nlme` (Pinheiro *et al.*, 2023) packages. Indirect paths were calculated by

220 multiplying component path coefficients, and error terms for indirect effects were
 221 calculated using the delta method with the `msm` package (Christopher H. Jackson, 2011)
 222 (see Supplementary Methods).

223 Results

224 Full Time Series

225 Across the 22-year time series, the majority of communities were compensatory ($VR < 1$),
 226 which was accentuated by soil disturbance and nitrogen addition (Fig. 1A). Synchrony was
 227 reduced in plots under low to moderate levels of nitrogen addition; however, synchrony across
 228 disturbance regimes converged at high nitrogen levels. Therefore, this linear relationship
 229 (quadratic model $AIC = 36.10$, linear model $AIC = 12.04$) exhibited a weakened effect of
 230 disturbance on synchrony in high nitrogen plots (Fig. 1A). In control plots, soil disturbance
 231 decreased synchrony by 0.21 ± 0.04 on average (mean effect across fields; $t(2) = -4.76$,
 232 $p = 0.04$, Table S2). In contrast, synchrony in disturbed plots receiving the highest nitrogen
 233 treatment did not significantly differ from intact plots (difference in synchrony = 0.01 ± 0.07 ,
 234 $t(2) = 0.14$, $p = 0.90$). These compensatory temporal dynamics can be observed among
 235 dominant species; particularly, C3 grasses *Agropyron repens* and *Poa pratensis* exhibited
 236 pairwise compensatory dynamics, especially under high nitrogen (Fig. 2).

237 Nitrogen addition consistently increased compensatory dynamics by affecting aggregate
 238 population variability moreso than community variability across disturbance regimes.
 239 Nitrogen addition resulted in communities with greater population variability (Fig. 3A;
 240 effect of nitrogen addition: $\hat{\beta} = 0.03 \pm 0.003$, $t(236) = 12.29$, $p < 0.01$, Table S4). However,
 241 nitrogen addition also increased community variability (Fig. 3A; effect of nitrogen
 242 addition: $\hat{\beta} = 0.02 \pm 0.002$, $t(236) = 6.66$, $p < 0.01$, Table S5). The effect of soil
 243 disturbance on population and community variability was also estimated to be positive but

with greater uncertainty (effect on population variability: $\hat{\beta} = 0.04 \pm 0.03$, $t(2) = 2.40$, $p = 0.32$; effect on community variability $\hat{\beta} = 0.07 \pm 0.03$, $t(2) = 1.30$, $p = 0.14$)

Stability decreased with increased nitrogen concentration (Fig. 1B, effect in intact plots: $\hat{\beta} = -0.03 \pm 0.005$, $t(208) = -6.29$, $p < 0.01$, Table S3), and disturbance did not significantly alter the nitrogen-stability relationship (main effect; $\hat{\beta} = 0.03 \pm 0.14$, $t(2) = 0.23$, $p = 0.84$, interaction; $\hat{\beta} = 0.002 \pm 0.008$, $t(208) = 0.21$, $p = 0.83$). The nitrogen-stability relationship showed a linear trend (Fig. 1B, linear model AIC = 371.8, quadratic model AIC = 397.7). The highest level of nitrogen decreased stability by an average of 0.74 ± 0.17 ($t(196) = -4.37$, $p < 0.01$) compared to the control (Fig. 1B). This decrease in biomass stability is observed in temporal trends of dominant species, with increased mean biomass coupled with more variability through time in fertilized plots (Fig. 2).

At low to moderate nitrogen levels ($0 - 5.4 \text{ g N} \cdot \text{m}^2 \cdot \text{year}^{-1}$), the mean and standard deviation of community biomass similarly change, maintaining stability equivalent to reference levels (i.e. control; Fig. 3B, points fall along the black reference line). Meanwhile, biomass variability at high nitrogen levels increased through time, resulting in decreased stability (effect of $9.5 \text{ g N} \cdot \text{m}^2 \cdot \text{year}^{-1}$ on the standard deviation in total biomass: $\hat{\beta} = 56.084 \pm 8.437$, $t(196) = 6.65$, $p < 0.01$, for additional nitrogen effects on stability and its components see Tables S6, S7, S8). At high nitrogen levels, increases in biomass variability exceeded the increase in the mean, yielding decreased stability.

Successional Dynamics

While the synchrony-stability relationship was consistently negative, the strength of the relationship depended on the interplay between disturbance and nitrogen addition (Fig. 4). In undisturbed plots, the synchrony-stability relationship remained stable across time and nitrogen treatment (Fig. S2). In comparison, disturbance caused an initial strengthening of this relationship (i.e., a more negative slope, $\hat{\beta} = -3.19 \pm 0.92$ with disturbance versus

$\hat{\beta} = -1.70 \pm 0.67$ without disturbance), but its effect weakened at intermediate nitrogen levels during the transient period (Fig. S2). Therefore, disturbed plots settled on weaker synchrony-stability relationships than their undisturbed counterparts ($\hat{\beta} = -0.65 \pm 0.33$ with disturbance versus $\hat{\beta} = -1.80 \pm 0.50$ without disturbance).

The SEMs confirmed that the effects of nitrogen addition and disturbance differed between the two successional periods (Fig. 5, Tables S9, S10). During the transient phase, nitrogen addition decreased synchrony (standardized path coefficient of -0.20 ± 0.08 , $p = 0.01$) and stability (-0.35 ± 0.06 , $p < 0.01$). In contrast, during the post-transient phase, the direct effect of nitrogen on synchrony was weakly positive (0.15 ± 0.10 , $p = 0.11$) while maintaining strong negative effects on stability (-0.29 ± 0.07 , $p < 0.01$). Similarly, synchrony mediated the nitrogen-stability relationship in the transient phase (indirect path coefficient of 0.14 ± 0.07 , $p = 0.02$); yet, the strength of the estimated mediation effect decreased post-transience (indirect path coefficient of -0.08 ± 0.06 , $p = 0.08$). During the transient phase, synchrony strongly mediated the disturbance-stability relationship (indirect path coefficient of 0.53 ± 0.12 , $p < 0.01$). The SEMs also confirmed that disturbance had strong negative effects on both synchrony (-0.79 ± 0.12 , $p = 0.02$) and stability (-0.56 ± 0.12 , $p = 0.04$) in the transient phase (Fig. 5A), but these effects eroded post-transience, in contrast to the stronger estimated impact of nitrogen addition.

Global change drivers not only had strong relationships with synchrony and stability but also impacted community biodiversity. Nitrogen addition had strong, persistent, negative relationships with species richness across periods (transient: -0.64 ± 0.04 , $p < 0.01$; post-transient: -0.52 ± 0.04 , $p < 0.01$; Fig. 5). Richness significantly mediated the nitrogen-stability relationship in the transient phase (indirect path coefficient of -0.10 ± 0.05 , $p = 0.02$), but not post-transience (indirect path coefficient of -0.04 ± 0.05 , $p = 0.21$). The effect of nitrogen addition on species evenness increased through time (transient: -0.27 ± 0.09 , $p < 0.01$; post-transient: -0.54 ± 0.08 , $p < 0.01$), becoming as strong as the effect on

species richness during the post-transient period. In contrast, the effect of disturbance on biodiversity diminished through time (Tables S9 S10), paralleling its effects on synchrony and stability. Given the persistently weak effects disturbance had on richness, it follows that richness did not mediate the disturbance-stability relationship (indirect transient path coefficient of -0.02 ± 0.05 , $p = 0.36$, indirect post-transient path coefficient of -0.005 ± 0.01 , $p = 0.34$).

Community diversity and synchrony affected stability patterns in the transient and post-transient phases. Initially, evenness was negatively related to stability (-0.10 ± 0.04 , $p = 0.03$), while richness exhibited a positive effect (0.16 ± 0.07 , $p = 0.02$); however, both effects eroded in the post-transient period. In contrast, synchrony had a consistent, strongly negative effect on stability (transient: -0.67 ± 0.05 , $p < 0.01$; post-transient: -0.55 ± 0.05 , $p < 0.01$). See Supplementary Results for SEMs that decompose synchrony and stability into their main components: community variance, population variance, and mean total biomass (Fig. S4).

Discussion

Our long-term study demonstrated that exposure to pulse disturbance and press nitrogen addition interactively affects the synchrony and stability of temperate grassland communities. Disturbance lowered community synchrony, but only when nitrogen concentrations were sufficiently low. Higher rates of nitrogen addition led to compensatory dynamics, regardless of disturbance history. Despite the stabilizing potential of compensatory dynamics, nitrogen addition decreased community stability, primarily because the effects of nitrogen shifted from promoting biomass at low concentrations to promoting variability at high concentrations. The effects of disturbance and nitrogen addition were also dependent on the stage of succession. In the early transient phase,

disturbance and nitrogen treatments negatively affected richness, evenness, synchrony, and stability. In contrast, in the post-transient phase—more than a decade into the experiment—press nitrogen addition maintained strong negative effects on richness, evenness, and stability, while pulse disturbance effects were no longer detectable. The timeline of this shift corresponds with the gradual replacement of early-successional species by later-successional C3 grasses (Seabloom *et al.*, 2020), which were more abundant and variable in high nitrogen treatments. Our study reveals that expected relationships between synchrony and stability are dynamic, signifying that these well-established links cannot always reliably predict the effects of global change on communities if they themselves are vulnerable to change. Additionally, overall community responses to global change may emerge and interact at differing temporal scales, requiring long-term data to disentangle.

Our investigation demonstrated that, though the synchrony-stability relationship remained negative, the consequences of soil disturbance and nitrogen addition on synchrony did not result in a subsequent positive influence on stability. Instead, stability and synchrony were both directly and negatively impacted, altering the relationship strength (Figs. 1, 4). Disturbance at low nitrogen levels induced compensation as aggregated population variance increased when species turnover rates surged post-disturbance (Fig. 3, Seabloom *et al.*, 2020; DeSiervo *et al.*, 2023), deviating from our hypothesized outcome of increased synchrony (Table S1 H6). However, nitrogen addition decreased synchrony as expected (Table S1 H2), likely by benefiting few species and increasing competition (Tilman, 1990), intensifying compensatory dynamics between dominants (Lepš *et al.*, 2019). Overall, the predicted negative synchrony-stability relationship weakened over time and effectively decoupled at high nitrogen levels (Figs. 1, 4, 5). Following soil disturbance, a strong increase in plant community biomass was sustained by consistent nitrogen addition in fertilized plots (Tilman, 1987; Inouye & Tilman, 1988). Therefore, despite the

diminishing effect of disturbance on plant biomass (Fig. S4), the decoupling phenomenon persisted into the post-transient phase due to continuous nitrogen input, showcasing how global change drivers maintained lagged synchrony and stability dynamics.

In addition to direct effects on stability, indirect pathways mediated community stability under global change. With synchrony acting as a mediator of the disturbance-stability relationship, we expected that any factor that decreased synchrony would positively affect stability, due to synchrony's inverse relationship with stability (Loreau & de Mazancourt, 2013). As such, though the effects of disturbance on all community properties diminished in the post-transient phase (Fig. 5B), we found a strongly positive indirect effect of disturbance on stability when mediated by synchrony in the transient phase. This indirect positive effect canceled out direct negative impacts of disturbance on stability (Fig. 5A), explaining the apparent lack of effect of soil disturbance on stability that arose in our best-fit models (Fig. 1B, Fig. S3D), and highlighting the analytical value of decomposing relationships into direct and indirect effects. This result carries important implications for considering synchrony in other ecosystems. For example, indirect effects of global change mediated by synchrony could have negative downstream impacts on community stability when drivers such as temperature, precipitation, or grazing pressure also alter synchrony (Parmesan 2006; Valencia *et al.*, 2020a; Ebel *et al.*, 2022).

Though nitrogen addition had strong negative direct effects on stability throughout succession (Fig. 5), they were dampened when mediated by species richness—so much so that nitrogen addition had an insignificant indirect effect on stability when mediated by richness in the post-transient phase. This finding supports the diversity-stability hypothesis (Elton, 1958; Odum, 1953), which suggests diverse communities are more likely to have several weakly interacting species, rather than a few species whose strong interactions destabilize community dynamics (McCann 2000). In this instance, our results suggest that the mechanism by which nitrogen addition decreased community stability was

by decreasing species richness (DeSiervo *et al.*, 2023; Seabloom *et al.*, 2020), which resulted in the emergence of two C3 grass species that dominantly contributed to fluctuations in total biomass (Fig. 2). The negative effects of nitrogen addition on biodiversity persisted as nitrogen treatments were applied annually, continuously favoring dominant species.

We additionally considered the role of species evenness in the diversity-stability relationship, as evenness is often an overlooked but important predictor of stability (Hillebrand *et al.*, 2008). When communities were in transience following disturbance, plots exhibited greater evenness as species competed to establish in the newly created habitat. However, after communities had settled on their equilibrium, nitrogen addition forced a dominance structure that favored few species (Tilman, 1990), making them less even over time. This explains the strong negative relationship between richness and evenness in the post-transient phase (Fig. 5B). Overall, we found that global change drivers could dampen the positive relationship between diversity and stability by reducing portfolio effects and evenness.

In systems undergoing succession, relationships between community properties are expected to shift in direction and magnitude over time, thus motivating the need to examine global change impacts on diversity, synchrony, and stability across long-term time series. The grasslands at Cedar Creek exhibited transience since the initial application of experimental treatments, but settled on dynamical equilibria after approximately a decade (DeSiervo *et al.*, 2023), thus motivating partitioning the time series into transient- and post-transient phases. Additionally, the effects of global change themselves may differ through time, necessitating additional scrutiny of how these dynamic patterns yield different community responses at varying points in time. For example, global change can induce different disturbance regimes, which may recruit different species over the course of observation and affect community composition across long periods (Benincà *et al.*, 2015). The necessity of long-term data to study successional phases then becomes highly apparent

for drawing robust conclusions about how dynamic community relationships may change through time, as evidenced by the emergence of a strong richness-evenness relationship in the post-transient phase, and the decreased effect of soil disturbance on synchrony and stability over time (Fig. 5). Furthermore, long-term data is particularly important to studies on synchrony, as best practice for calculating synchrony measures requires sufficiently long time series. Analyzing short time series may instead result in erroneous conclusions about a community's synchrony, as they will bias results to show more synchronous than compensatory dynamics (Valencia *et al.*, 2020b; Luo *et al.*, 2021). In our study, long-term data was doubly imperative for calculating not just one, but two phases of synchrony.

By examining the multidimensional impacts of global change drivers on community dynamics, we find that nitrogen addition and soil disturbance decrease synchrony and stability, and can change the magnitude and direction of diversity-stability relationships through time. However, these changes will likely depend on species traits and environmental variability, where we expect annually-dominated systems to show quicker responses and greater synchrony than perennially-dominated systems (Shoemaker *et al.*, 2022; Werner *et al.*, 2024). Nevertheless, this result mirrors changes in several grassland systems across multiple continents, where global change drivers have restructured community compositions and competitive hierarchies (Avolio *et al.*, 2021), affecting ecosystem productivity despite several cases where species richness was maintained (Komatsu *et al.*, 2019; Avolio *et al.*, 2014). These impacts may also be lagged, where ecosystems may appear resilient to change in the short term but are strongly affected long term (Komatsu *et al.*, 2019), requiring lengthy datasets to properly understand these time-sensitive shifts. For example, following theory, we found the synchrony-stability relationship to be strongly linked in the transient phase, but was decoupled post-transience by the interactive effect of global change drivers. These results have future implications on

how diversity and synchrony may be used to predict effects on stability in systems undergoing global change, particularly over long time series. As such, incorporating synchrony into future research on long-term impacts of global change drivers remains crucial for understanding the direct and indirect mechanisms by which global change affects dynamic community relationships.

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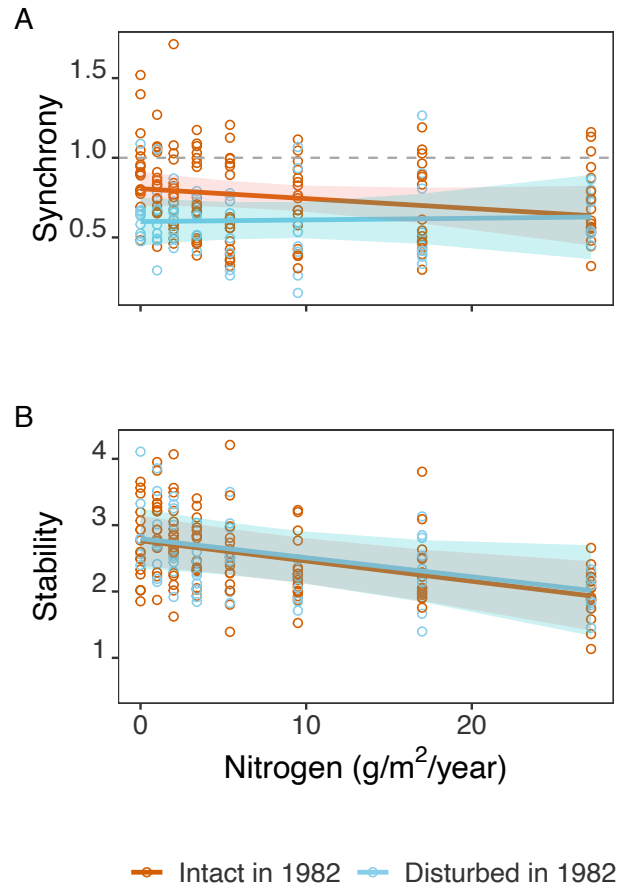


Figure 1: Synchrony is measured as a variance ratio (A), and community stability is measured as the inverse coefficient of variation (B) across global change treatments. (A) shows the linear relationship of synchrony with nitrogen addition and disturbance (colors). The dotted line represents a variance ratio (VR) of 1, which indicates the transition from synchronous (VR>1) to compensatory (VR<1) dynamics. (B) stability has a negative linear relationship with nitrogen. Shaded regions represent 95% confidence intervals. Best fit lines are averaged across field using `emmeans` (Lenth, 2023). Model summaries are in Supplementary Tables, S2 and S3.

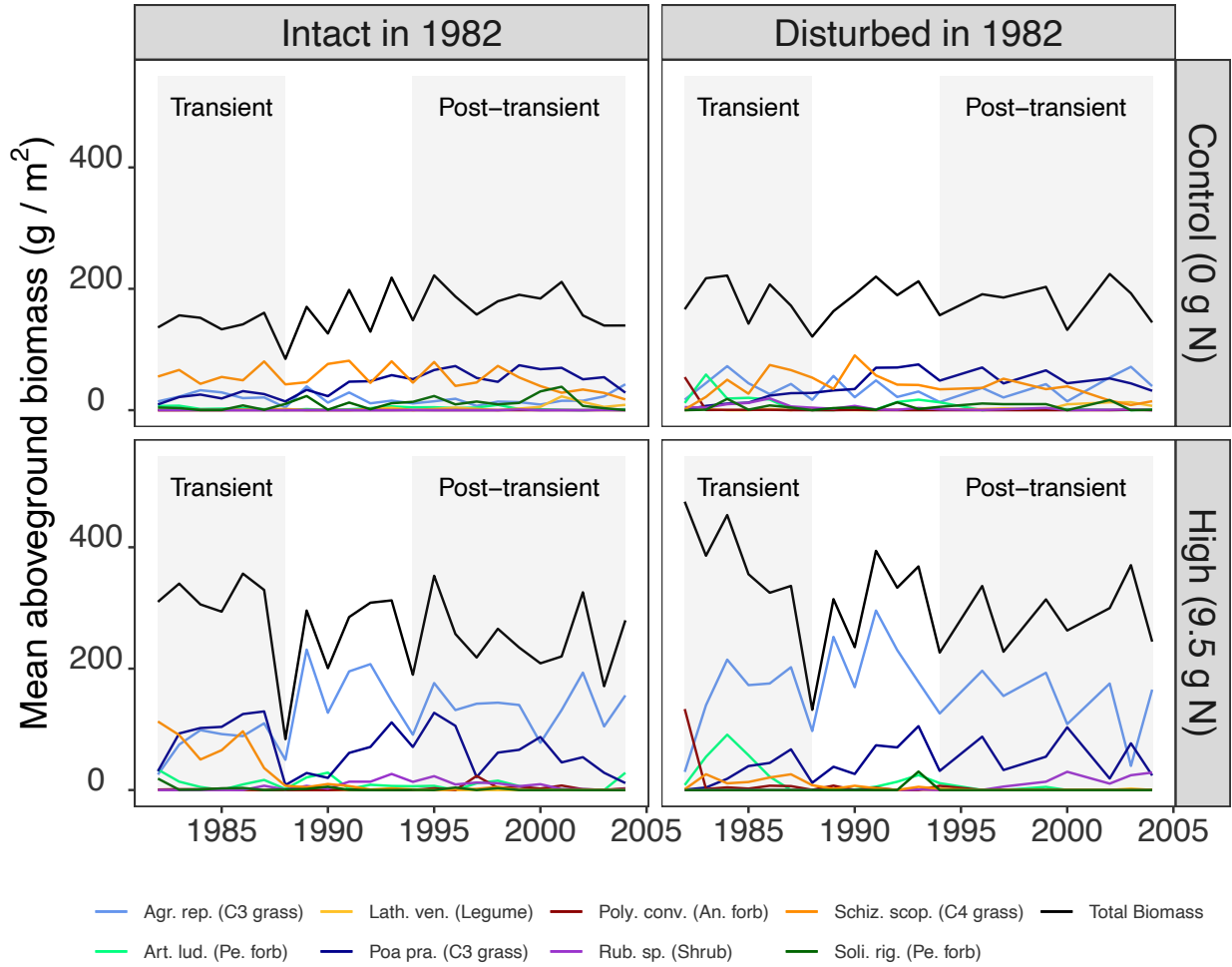


Figure 2: Average total above-ground biomass (black line) and biomass of the top one or two most abundant species from different functional groups (colored lines) in control plots ($0 \text{ g N} + \mu$) and fertilized plots ($9.5 \text{ g N} + \mu$) and intact (left) and disturbed plots (right) through time. Positively correlated fluctuations in biomass among species indicate pairwise synchronous dynamics, while negatively correlated fluctuations indicate pairwise compensatory dynamics. Smaller fluctuations in total biomass (black) indicate higher stability. Shaded regions indicate the time periods used in Fig. 4 and 5, with the transient phase as the period directly after disturbance and the post-transient phase after the system has settled into a steady state. Species names and some functional groups are abbreviated with An. forb = annual forb, Pe. forb = perennial forb, and Shrub = low lying shrub.

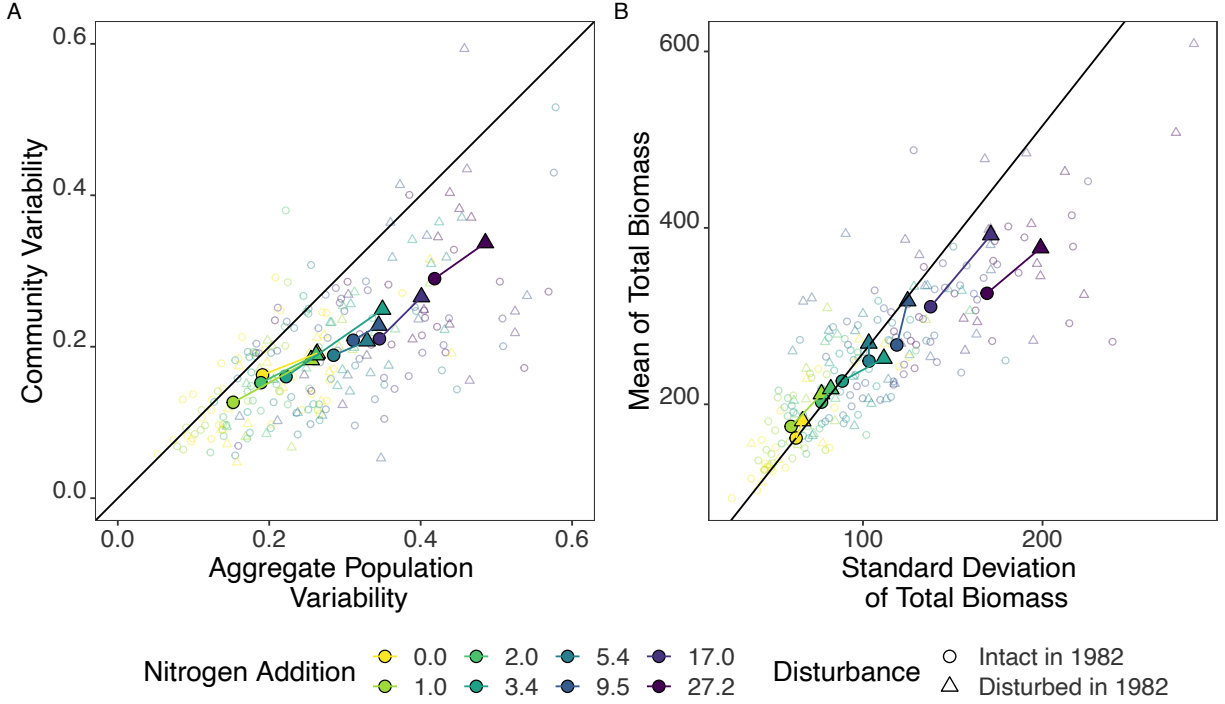


Figure 3: Scatter plot of the two components of the variance ratio (A) used to measure community synchrony and the two components of the inverse coefficient of variation (B), used to measure stability. The filled-in circles and triangles represent the mean per treatment, while faint circles and triangles show raw data. Community variability (vertical axis, A) is measured as the variance of the total biomass of the community through time and comprises the numerator of the variance ratio. Aggregate population variability (horizontal axis, A) is the sum of the temporal variances of each population in the community and comprises the denominator. If populations fluctuate independently through time, then the sum of the temporal variances of the populations will equal the temporal variance of the sum and points will fall along the black 1:1 line. The area above the line denote synchronous dynamics while the area below the line denotes compensatory dynamics. In (B), the black line denotes the stability of the control plot (i.e. no disturbance, $0\text{ N} + \mu$), with the area above showing increased stability compared to the control and the area below showing decreased stability.

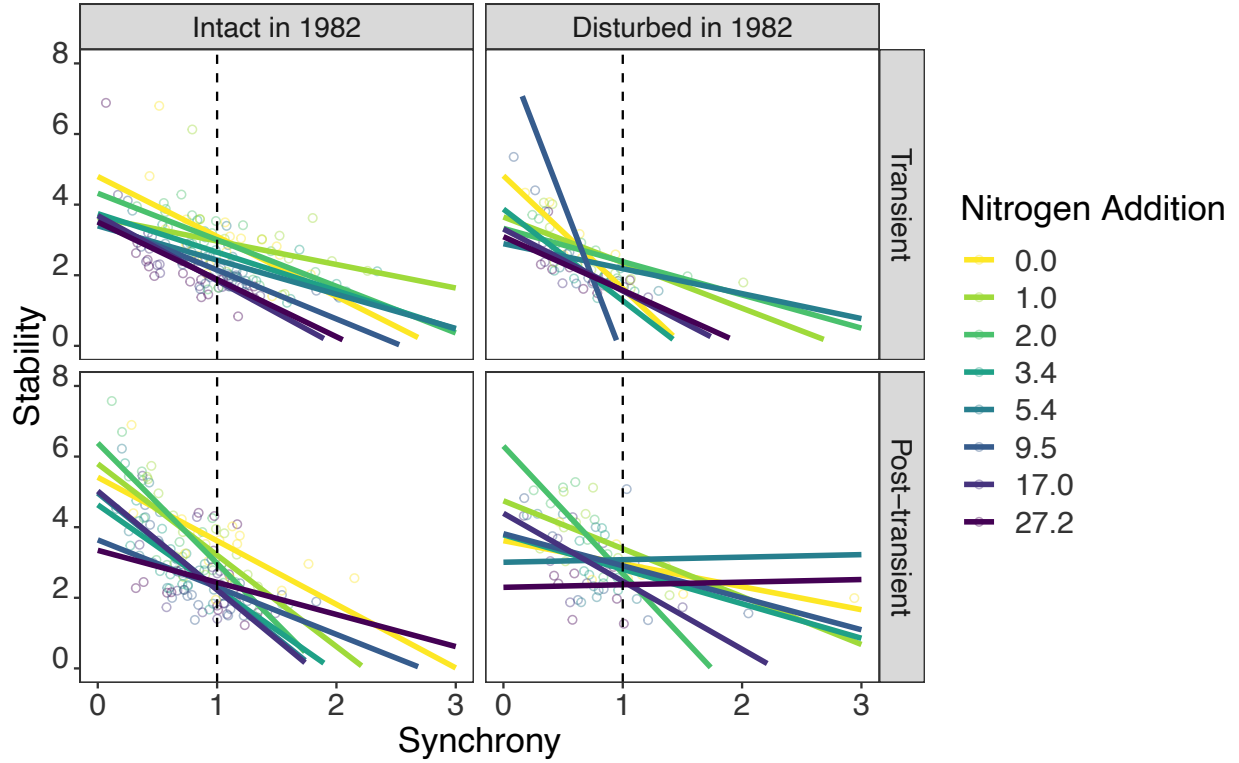


Figure 4: Synchrony and temporal stability across communities over the 22 year time series, dependent on nitrogen addition (colors), disturbance treatments (columns), and successional phase (rows). The dotted, vertical line represents independent fluctuations ($VR = 1$), separating compensatory (left of the line) from synchronous dynamics (right of the line). Confidence intervals for intercepts and slopes are shown in Figure S2. While the synchrony-stability relationship remains overall negative through time and across global change treatments, the post transient phase (lower panels, shows a more more variable relationship, especially in disturbed plots.

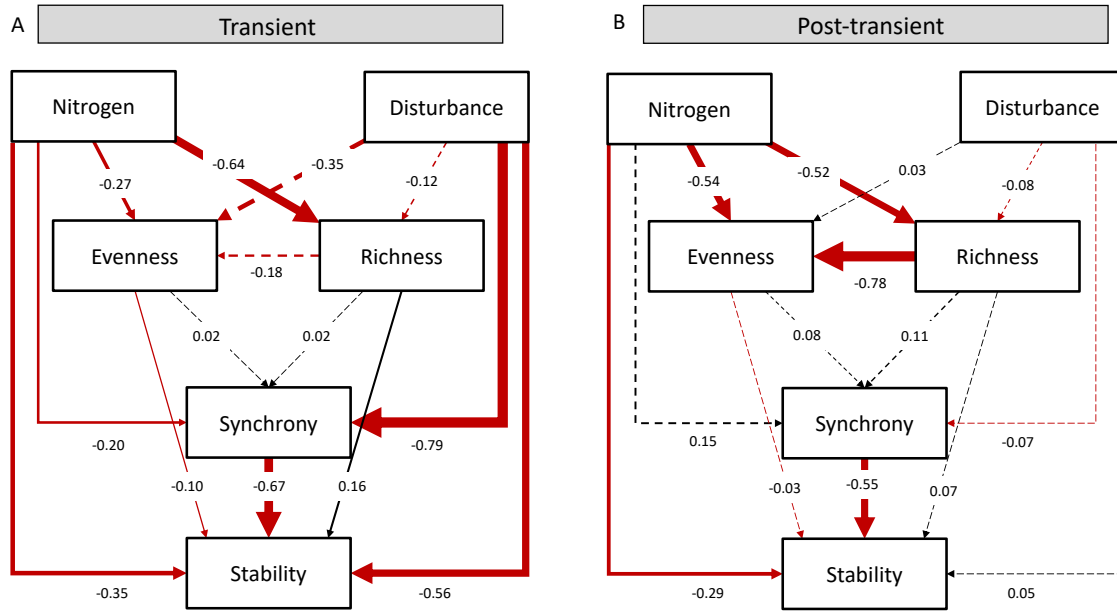


Figure 5: Path diagrams of the structural equation models fit to data collected (A) during the transient phase (1982-1988) and (B) after the transient phase (1994, 1996-1997, 1999-2000, 2002-2004). Both SEMs are fully saturated ($\chi^2 = 0.0$, $df = 0.0$). Values next to each arrow indicate the standardized coefficient of the direct effect. Red arrows indicate negative relationships, while black arrows indicate positive relationships. Dashed arrows indicate paths that were included in the model fit, but for which the 95% confidence intervals for the path coefficients overlap zero. The widths of the arrows are proportional to the magnitude of each relationship. Summaries of direct effects can be found in Tables [S9](#) and [S10](#).

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