

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.

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1 Abstract

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

15 Introduction

16 Global change drivers such as agricultural disturbances, fertilization, atmospheric nutrient
17 deposition, and warming temperatures threaten ecosystems around the world (Pounds
18 *et al.*, 2006; Stevens *et al.*, 2010; Pachauri *et al.*, 2014). Global change drivers alter
19 multiple community assembly processes, ultimately altering the maintenance of species
20 richness and the stability of biomass production (Tilman 1985; Muehleisen *et al.*, 2022),
21 with simultaneous global change drivers yielding strong, interactive effects (Zhu *et al.*,
22 2016; Collins *et al.*, 2022; Komatsu *et al.*, 2019). While the independent and interactive
23 effects of global change drivers on ecological diversity and stability have been well explored
24 (Tilman, 1985; Komatsu *et al.*, 2019; Avolio *et al.*, 2021), the impact of multiple

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

31 Global change drivers commonly impact community composition, including diversity
32 and evenness patterns. For example, increased nutrient loading in grassland communities
33 shifts competitive hierarchies by decreasing native biodiversity and increasing invasive
34 species dominance (Stevens *et al.*, 2004; Borer *et al.*, 2017; Tilman 1985; Seabloom *et al.*,
35 2020). These changes in dominance and local extinction events are driven by species' direct
36 responses to global change and environmentally-induced changes in species interaction
37 strengths (Collins *et al.*, 2022; Weiss-Lehman *et al.*, 2022). Therefore, shifting community
38 compositions likely result from multiple consequences of global change, including species
39 loss/gain, changes in evenness, and species reordering, which can occur on different
40 timescales (Avolio *et al.*, 2021). Furthermore, shifts in community composition under
41 global change often negatively impact ecosystem stability (Tilman *et al.*, 1996; Hautier
42 *et al.*, 2015); for example, fertilization increased interannual variability of biomass across
43 global grasslands (Carroll *et al.*, 2022).

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

51 [1994; Ives *et al.*, 1999; Valencia *et al.*, 2020a]. Conversely, compensatory dynamics are the
52 tendency for periods of low abundance of some species to be offset by high abundance in
53 other species and are often driven by strong competition or opposing responses to
54 environmental fluctuations, thereby increasing stability (Ives *et al.*, 1999; Yachi & Loreau,
55 1999; Loreau & de Mazancourt, 2013). Theory predicts that shifts in dominance and
56 species richness alter temporal stability via changes in synchrony (Doak, 1998; Tilman,
57 1998). Higher richness increases a community’s portfolio and the likelihood of species
58 responding differently to fluctuating environments, decreasing synchrony and increasing
59 stability. If global change drivers impact portfolio effects, they could have downstream
60 repercussions on synchrony and stability.

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

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

80 Understanding synchrony and stability in grasslands is crucial due to their significant
81 roles in food supply (O'Mara, 2012), carbon sequestration (Soussana *et al.*, 2004), and
82 other ecosystem services (Bengtsson *et al.*, 2019). Temperate grasslands face extensive
83 land-use alterations (Mock, 2000; Newbold *et al.*, 2016), while contending with widespread
84 nutrient increases from agricultural runoff and atmospheric nitrogen deposition (Gruber &
85 Galloway, 2008). Here, we examine how multiple global change drivers—nitrogen addition
86 coupled with soil disturbance—impact grassland community synchrony, stability, and
87 diversity across successional timescales. We use data from a 22-year fully factorial
88 grassland experiment at the Cedar Creek Ecosystem Reserve in Minnesota, USA. We build
89 on previous work from Cedar Creek showing changes in species richness and community
90 composition under disturbance and nitrogen addition (Seabloom *et al.*, 2020), and that the
91 system recovered to novel, nutrient-mediated equilibria after approximately a decade of
92 transient dynamics (DeSiervo *et al.*, 2023). We ask: (1) How do disturbance and nitrogen
93 addition alter community synchrony? (2) To what extent do community properties of
94 richness, evenness, and synchrony jointly alter community stability with multiple global
95 change drivers? and (3) How do these relationships change through succession? We
96 hypothesized that disturbance would increase community synchrony (Table S1, H6), but
97 nitrogen addition may increase or decrease synchrony (Table S1, H2), dependent on
98 changes in species interactions. Nitrogen addition and soil disturbance were expected to
99 decrease stability (Table S1, H1, H5) by increasing biomass in favorable years of growth
100 (Lee *et al.*, 2010), leading to larger synchronized booms and busts in species biomass. We
101 also expected decreased richness due to nitrogen addition and disturbance (Seabloom *et al.*,
102 2020) would decrease stability due to portfolio loss (Lehman & Tilman, 2000; Loreau *et al.*,

103 [2021](#), [Doak](#), [1998](#)).

104 **Materials and Methods**

105 **Study Site and Data Collection**

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

111 We briefly describe the experiment, with additional details in [Tilman](#) ([1987](#)) and
112 [Seabloom *et al.*](#) ([2020](#)). In 1982, identical nutrient addition experiments were established
113 within two grids (35 x 55 m), replicated in three agricultural fields that were abandoned in
114 1968 (Field A), 1957 (Field B), and 1934 (Field C). Old field vegetation was left intact in
115 one grid within each field (E001) ([Tilman](#), [2021b](#)), while the other grid was disked to
116 disturb the soil and restart succession in the spring of 1982 (E002) ([Tilman](#), [2021a](#)). Each
117 grid was split into 54 vegetation plots (4 X 4 m) for a total of 324 plots. Six replicate plots
118 within each grid received one of nine nutrient addition treatments annually. Nutrient
119 addition treatments included a control (no nutrient addition), micronutrients (μ) only, and
120 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.
121 Nitrogen was added annually as NH₄NO₃, and micronutrients (μ) consisted of P, K, Ca,
122 Mg, S, and citrate-chelated trace metals (see Supplementary Methods for detailed
123 micronutrient amounts). We used the 0 g N + μ \cdot m² \cdot year⁻¹ as our control for analyses to
124 hold the addition of micronutrients constant (see Supplementary Methods, Comparison of
125 Control Conditions).

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

127 dried, and weighed to the nearest 0.01 g. All plots were sampled annually from 1982 to
128 2004, except for 1995 (only E001 sampled), 2001 (only E001 sampled), and 2003 (only
129 E001 and Field C in E002 sampled). From 1992 onwards, three plots were randomly
130 assigned to different nutrient cessation or burning treatments in each field. These plots
131 were omitted from our analyses, resulting in 216 total. We analyzed species level and
132 aggregated community biomass, removing woody species except for low-lying shrubs (see
133 Supplementary Methods, Data Cleaning). Finally, we visualized annual time series data for
134 the most abundant species of six functional groups (C4 grasses, C3 grasses, annual and
135 perennial non-leguminous forbs, legumes, and low-lying shrubs) in intact and disturbed
136 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
137 understand temporal trends in biomass.

138 Long-Term Time Series Analyses

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

144 The variance ratio is determined as:

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

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

$$148 \text{var}(C(t)) = \sum_{i=1}^N \text{var}(P_i(t)) + 2\sum_{i=1}^{N-1} \sum_{j=i+1}^N \text{cov}(P_i(t), P_j(t)).$$

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

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

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

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

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

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

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

176 Successional Dynamics

177 To determine the effect of global change drivers during transient early successional versus
178 post-transient dynamical-equilibria periods, we subdivided our time series into a transient
179 period that included data from 1982 to 1988 and a post-transient period using 1993 to 2004
180 data. We chose time windows encompassing seven years of data to facilitate cross-period
181 comparison while having long enough time series to obtain stable estimates of synchrony
182 and stability (e.g. [Hallett et al. 2014](#); [Zhao et al. 2020](#); [Walter et al. 2021](#)). We removed
183 1989 - 1992 to omit the compositional transition from succession to dynamical equilibria,
184 based on results from DeSiervo et al. ([2023](#)). Results are robust to different time series
185 windows (e.g., 7 versus 10-year). We fitted separate linear models within each combination
186 of nitrogen, disturbance treatment, and successional period to visualize variation in the
187 synchrony-stability relationship in the transient versus post-transient phases.

188 Community composition and species diversity also influence stability ([Tilman 1987](#)),
189 motivating us to examine direct and indirect pathways from soil disturbance and nitrogen
190 addition to biodiversity, synchrony, and stability using structural equation models (SEM).
191 We incorporated species richness and evenness as biodiversity metrics. We calculated species
192 richness by determining the maximum number of species censused annually in each plot and
193 averaging these per-plot richnesses across the years in transient and post-transient phases.
194 We evaluated species evenness using the E_{var} metric ([Smith & Wilson 1996](#)), which computes
195 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

244 with greater uncertainty (effect on population variability: $\hat{\beta} = 0.04 \pm 0.03$, $t(2) = 2.40$,
245 $p = 0.32$; effect on community variability $\hat{\beta} = 0.07 \pm 0.03$, $t(2) = 1.30$, $p = 0.14$)

246 Stability decreased with increased nitrogen concentration (Fig. 1B, effect in intact plots:
247 $\hat{\beta} = -0.03 \pm 0.005$, $t(208) = -6.29$, $p < 0.01$, Table S3), and disturbance did not significantly
248 alter the nitrogen-stability relationship (main effect; $\hat{\beta} = 0.03 \pm 0.14$, $t(2) = 0.23$, $p = 0.84$,
249 interaction; $\hat{\beta} = 0.002 \pm 0.008$, $t(208) = 0.21$, $p = 0.83$). The nitrogen-stability relationship
250 showed a linear trend (Fig. 1B, linear model AIC = 371.8, quadratic model AIC = 397.7).
251 The highest level of nitrogen decreased stability by an average of 0.74 ± 0.17 ($t(196) = -4.37$,
252 $p < 0.01$) compared to the control (Fig. 1B). This decrease in biomass stability is observed
253 in temporal trends of dominant species, with increased mean biomass coupled with more
254 variability through time in fertilized plots (Fig. 2).

255 At low to moderate nitrogen levels ($0 - 5.4 \text{ g N} \cdot \text{m}^2 \cdot \text{year}^{-1}$), the mean and standard
256 deviation of community biomass similarly change, maintaining stability equivalent to
257 reference levels (i.e. control; Fig. 3B, points fall along the black reference line). Meanwhile,
258 biomass variability at high nitrogen levels increased through time, resulting in decreased
259 stability (effect of $9.5 \text{ g N} \cdot \text{m}^2 \cdot \text{year}^{-1}$ on the standard deviation in total biomass:
260 $\hat{\beta} = 56.084 \pm 8.437$, $t(196) = 6.65$, $p < 0.01$, for additional nitrogen effects on stability and
261 its components see Tables S6, S7, S8). At high nitrogen levels, increases in biomass
262 variability exceeded the increase in the mean, yielding decreased stability.

263 Successional Dynamics

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

269 $\hat{\beta} = -1.70 \pm 0.67$ without disturbance), but its effect weakened at intermediate nitrogen
270 levels during the transient period (Fig. S2). Therefore, disturbed plots settled on weaker
271 synchrony-stability relationships than their undisturbed counterparts ($\hat{\beta} = -0.65 \pm 0.33$ with
272 disturbance versus $\hat{\beta} = -1.80 \pm 0.50$ without disturbance).

273 The SEMs confirmed that the effects of nitrogen addition and disturbance differed
274 between the two successional periods (Fig. 5, Tables S9, S10). During the transient phase,
275 nitrogen addition decreased synchrony (standardized path coefficient of -0.20 ± 0.08 ,
276 $p = 0.01$) and stability (-0.35 ± 0.06 , $p < 0.01$). In contrast, during the post-transient
277 phase, the direct effect of nitrogen on synchrony was weakly positive (0.15 ± 0.10 , $p = 0.11$)
278 while maintaining strong negative effects on stability (-0.29 ± 0.07 , $p < 0.01$). Similarly,
279 synchrony mediated the nitrogen-stability relationship in the transient phase (indirect path
280 coefficient of 0.14 ± 0.07 , $p = 0.02$); yet, the strength of the estimated mediation effect
281 decreased post-transience (indirect path coefficient of -0.08 ± 0.06 , $p = 0.08$). During the
282 transient phase, synchrony strongly mediated the disturbance-stability relationship
283 (indirect path coefficient of 0.53 ± 0.12 , $p < 0.01$). The SEMs also confirmed that
284 disturbance had strong negative effects on both synchrony (-0.79 ± 0.12 , $p = 0.02$) and
285 stability (-0.56 ± 0.12 , $p = 0.04$) in the transient phase (Fig. 5A), but these effects eroded
286 post-transience, in contrast to the stronger estimated impact of nitrogen addition.

287 Global change drivers not only had strong relationships with synchrony and stability but
288 also impacted community biodiversity. Nitrogen addition had strong, persistent, negative
289 relationships with species richness across periods (transient: -0.64 ± 0.04 , $p < 0.01$; post-
290 transient: -0.52 ± 0.04 , $p < 0.01$; Fig. 5). Richness significantly mediated the nitrogen-
291 stability relationship in the transient phase (indirect path coefficient of -0.10 ± 0.05 , $p =$
292 0.02), but not post-transience (indirect path coefficient of -0.04 ± 0.05 , $p = 0.21$). The effect
293 of nitrogen addition on species evenness increased through time (transient: -0.27 ± 0.09 ,
294 $p < 0.01$; post-transient: -0.54 ± 0.08 , $p < 0.01$), becoming as strong as the effect on

295 species richness during the post-transient period. In contrast, the effect of disturbance on
296 biodiversity diminished through time (Tables [S9](#) [S10](#)), paralleling its effects on synchrony
297 and stability. Given the persistently weak effects disturbance had on richness, it follows
298 that richness did not mediate the disturbance-stability relationship (indirect transient path
299 coefficient of -0.02 ± 0.05 , $p = 0.36$, indirect post-transient path coefficient of -0.005 ± 0.01 ,
300 $p = 0.34$).

301 Community diversity and synchrony affected stability patterns in the transient and
302 post-transient phases. Initially, evenness was negatively related to stability (-0.10 ± 0.04 ,
303 $p = 0.03$), while richness exhibited a positive effect (0.16 ± 0.07 , $p = 0.02$); however, both
304 effects eroded in the post-transient period. In contrast, synchrony had a consistent,
305 strongly negative effect on stability (transient: -0.67 ± 0.05 , $p < 0.01$; post-transient:
306 -0.55 ± 0.05 , $p < 0.01$). See Supplementary Results for SEMs that decompose synchrony
307 and stability into their main components: community variance, population variance, and
308 mean total biomass (Fig. [S4](#)).

309 Discussion

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

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

331 Our investigation demonstrated that, though the synchrony-stability relationship
332 remained negative, the consequences of soil disturbance and nitrogen addition on synchrony
333 did not result in a subsequent positive influence on stability. Instead, stability and
334 synchrony were both directly and negatively impacted, altering the relationship strength
335 (Figs. 1, 4). Disturbance at low nitrogen levels induced compensation as aggregated
336 population variance increased when species turnover rates surged post-disturbance (Fig. 3,
337 Seabloom *et al.*, 2020; DeSiervo *et al.*, 2023), deviating from our hypothesized outcome of
338 increased synchrony (Table S1 H6). However, nitrogen addition decreased synchrony as
339 expected (Table S1 H2), likely by benefiting few species and increasing competition
340 (Tilman, 1990), intensifying compensatory dynamics between dominants (Lepš *et al.*,
341 2019). Overall, the predicted negative synchrony-stability relationship weakened over time
342 and effectively decoupled at high nitrogen levels (Figs. 1, 4, 5). Following soil disturbance,
343 a strong increase in plant community biomass was sustained by consistent nitrogen
344 addition in fertilized plots (Tilman, 1987; Inouye & Tilman, 1988). Therefore, despite the

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

348 In addition to direct effects on stability, indirect pathways mediated community stability
349 under global change. With synchrony acting as a mediator of the disturbance-stability
350 relationship, we expected that any factor that decreased synchrony would positively affect
351 stability, due to synchrony's inverse relationship with stability (Loreau & de Mazancourt,
352 2013). As such, though the effects of disturbance on all community properties diminished in
353 the post-transient phase (Fig. 5B), we found a strongly positive indirect effect of disturbance
354 on stability when mediated by synchrony in the transient phase. This indirect positive effect
355 canceled out direct negative impacts of disturbance on stability (Fig. 5A), explaining the
356 apparent lack of effect of soil disturbance on stability that arose in our best-fit models
357 (Fig. 1B, Fig. S3D), and highlighting the analytical value of decomposing relationships
358 into direct and indirect effects. This result carries important implications for considering
359 synchrony in other ecosystems. For example, indirect effects of global change mediated
360 by synchrony could have negative downstream impacts on community stability when drivers
361 such as temperature, precipitation, or grazing pressure also alter synchrony (Parmesan 2006;
362 Valencia *et al.*, 2020a; Ebel *et al.*, 2022).

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

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

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

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

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

407 By examining the multidimensional impacts of global change drivers on community
408 dynamics, we find that nitrogen addition and soil disturbance decrease synchrony and
409 stability, and can change the magnitude and direction of diversity-stability relationships
410 through time. However, these changes will likely depend on species traits and
411 environmental variability, where we expect annually-dominated systems to show quicker
412 responses and greater synchrony than perennially-dominated systems (Shoemaker *et al.*,
413 2022; Werner *et al.*, 2024). Nevertheless, this result mirrors changes in several grassland
414 systems across multiple continents, where global change drivers have restructured
415 community compositions and competitive hierarchies (Avolio *et al.*, 2021), affecting
416 ecosystem productivity despite several cases where species richness was maintained
417 (Komatsu *et al.*, 2019; Avolio *et al.*, 2014). These impacts may also be lagged, where
418 ecosystems may appear resilient to change in the short term but are strongly affected long
419 term (Komatsu *et al.*, 2019), requiring lengthy datasets to properly understand these
420 time-sensitive shifts. For example, following theory, we found the synchrony-stability
421 relationship to be strongly linked in the transient phase, but was decoupled post-transience
422 by the interactive effect of global change drivers. These results have future implications on

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

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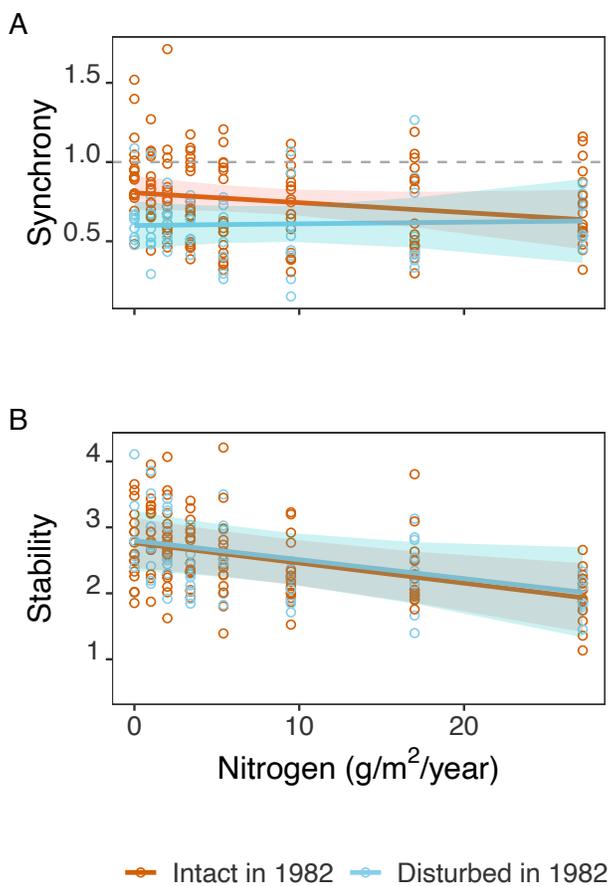


Figure 1: Synchrony is measured as a variance ratio (A), and community stability is measured as the inverse coefficient of variation (B) across global change treatments. (A) shows the linear relationship of synchrony with nitrogen addition and disturbance (colors). The dotted line represents a variance 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](#).

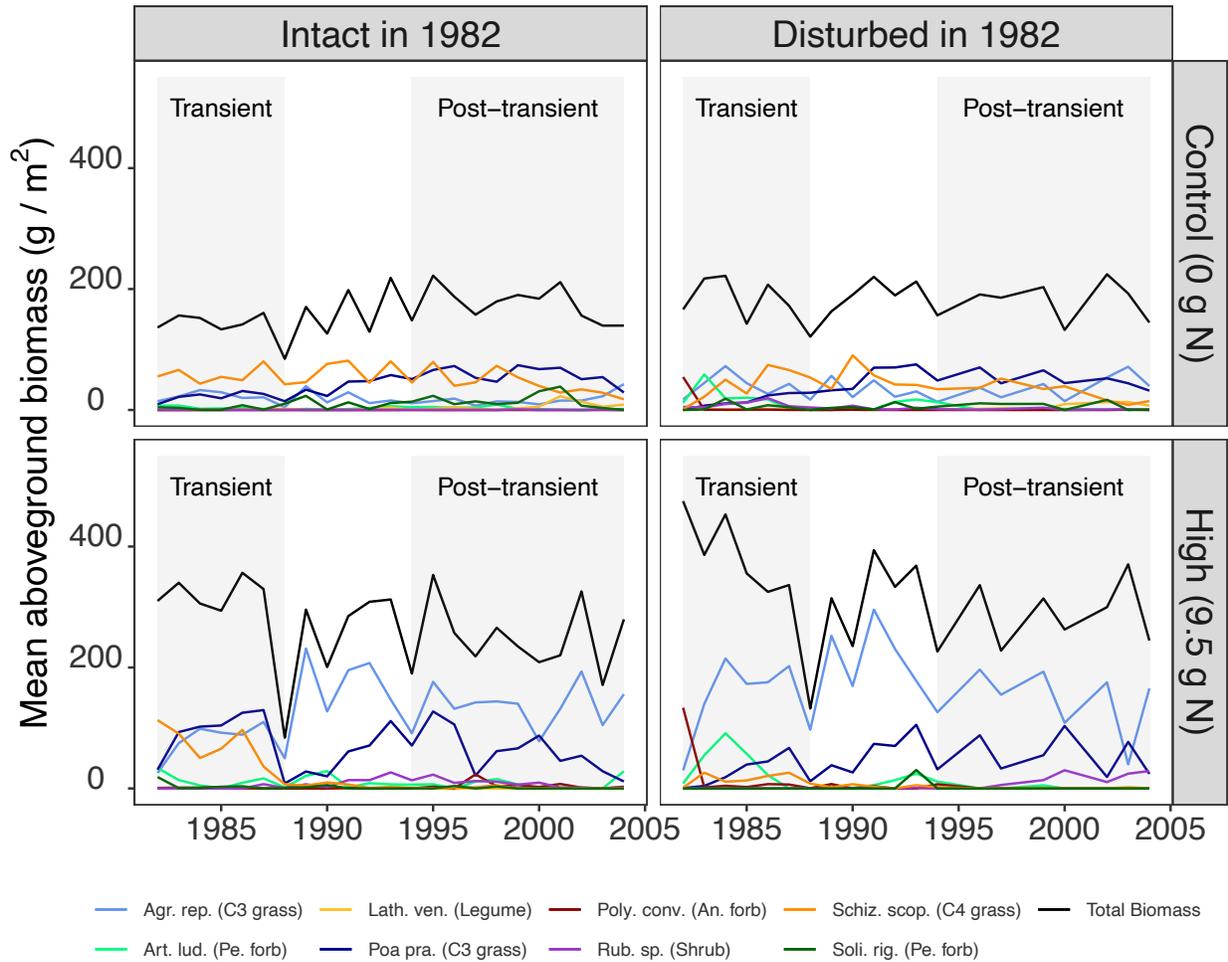


Figure 2: Average total above-ground biomass (black line) and biomass of the top one or two most abundant species from different functional groups (colored lines) in control plots ($0 \text{ g N} + \mu$) and fertilized plots ($9.5 \text{ g N} + \mu$) and intact (left) and disturbed plots (right) through 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.

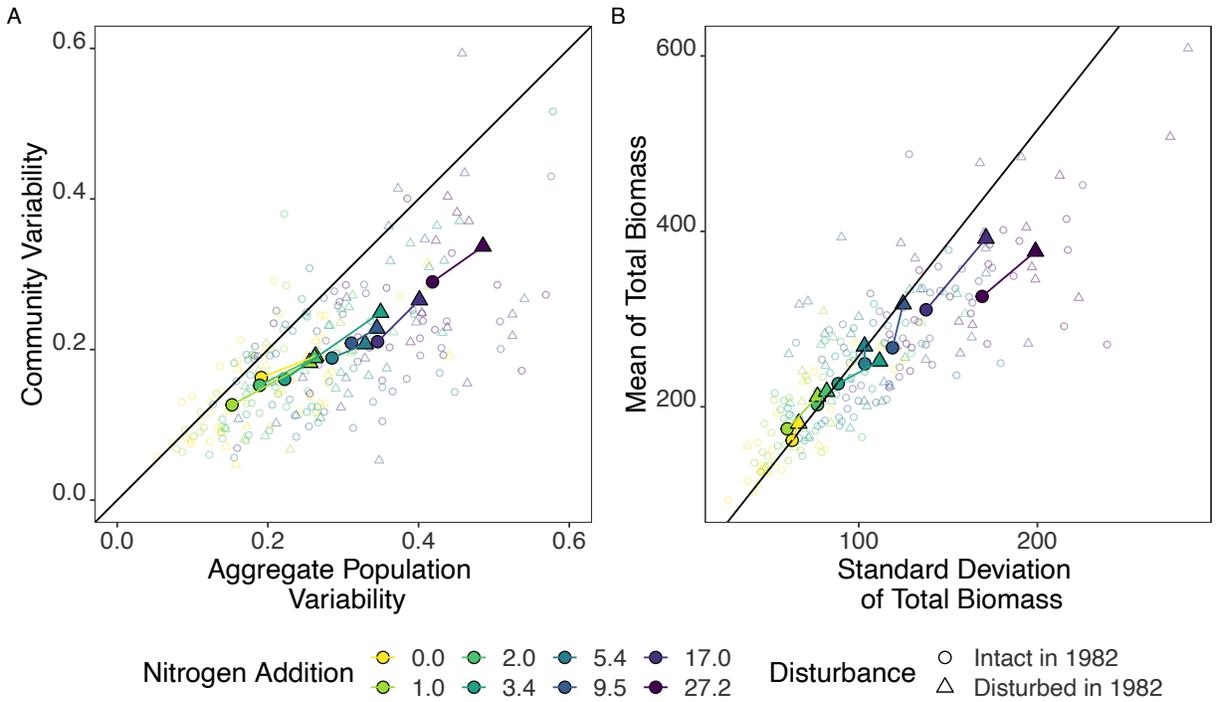


Figure 3: Scatter plot of the two components of the variance ratio (A) used to measure community synchrony and the two components of the inverse coefficient of variation (B), used to measure stability. The filled-in circles and triangles represent the mean per treatment, while faint circles and triangles 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.

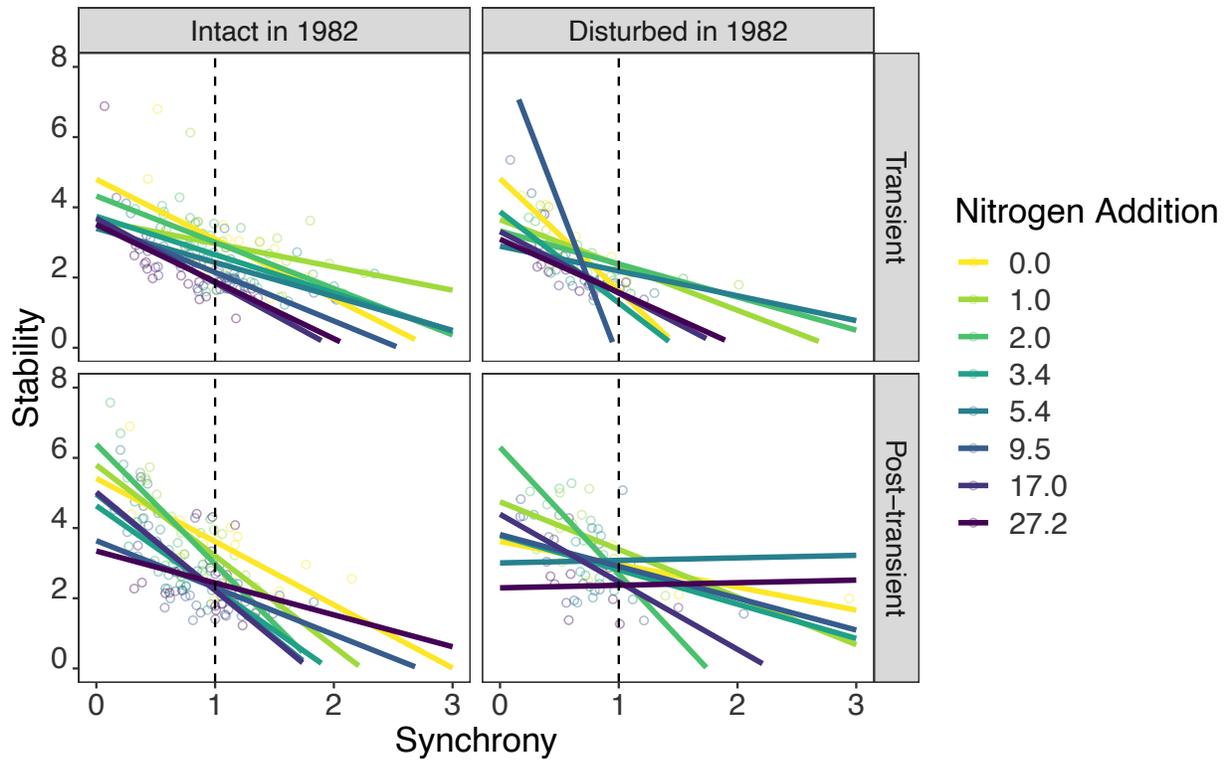


Figure 4: Synchrony and temporal stability across communities over the 22 year time series, dependent on nitrogen addition (colors), disturbance treatments (columns), and successional phase (rows). The dotted, vertical line represents independent fluctuations ($VR = 1$), separating compensatory (left 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.

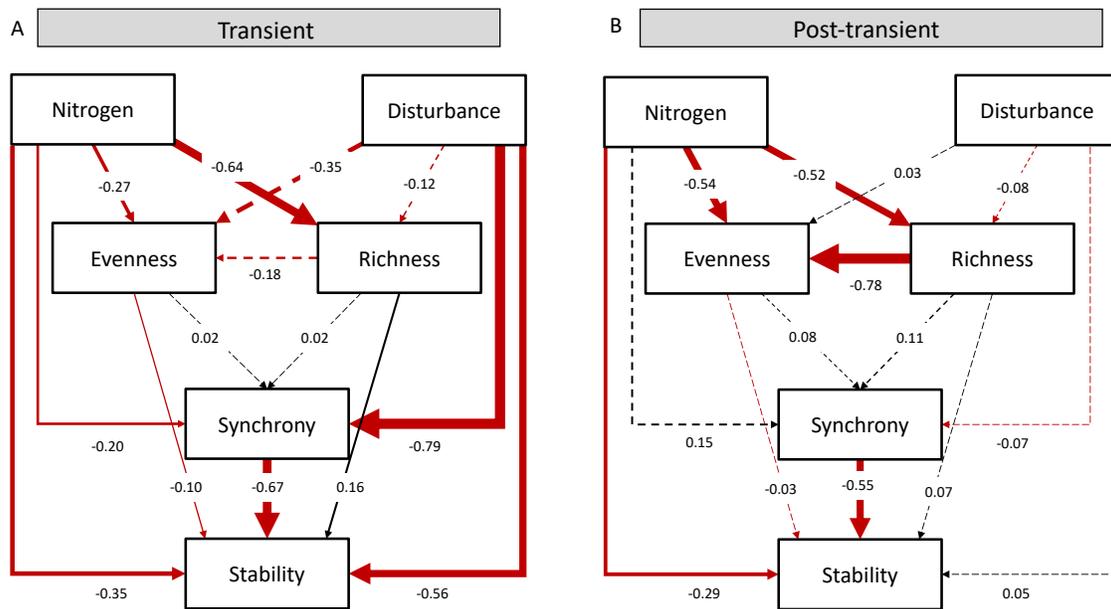


Figure 5: Path diagrams of the structural equation models fit to data collected (A) during the transient phase (1982-1988) and (B) after the transient phase (1994, 1996-1997, 1999-2000, 2002-2004). Both SEMs are fully saturated ($\chi^2 = 0.0, df = 0.0$). Values next to each arrow indicate the standardized 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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