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LETTER

Effects of Disturbance and Fertilisation on Plant Community Synchrony, Biodiversity and Stability Through Succession

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ABSTRACT

Global change drivers alter multiple components of community composition, with cascading impacts on ecosystem stability. However, it remains largely unknown how interactions among global change drivers will alter community synchrony, especially across successional timescales. We analysed 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, richness, evenness and stability during transient and post-transient periods of succession. Using multiple regression and structural equation modelling, we found that nitrogen addition and soil disturbance decreased both synchrony and stability, thereby weakening the negative synchrony–stability relationship. We found evidence of the portfolio effect during transience, but once communities settled on a restructured state post-transience, diversity no longer influenced the synchrony–stability relationship. Differences between transient and post-transient drivers of synchrony and stability underscore the need for long-term data to inform ecosystem management under ongoing global change.

1 | Introduction

Global change drivers such as soil tilling and fertilisation threaten ecosystems around the world, impacting multiple community assembly processes and ultimately altering the maintenance of species richness and the stability of biomass production (Tilman 1985; Stevens et al. 2010; Seabloom et al. 2021; Muehleisen et al. 2023). Simultaneous global change drivers often yield strong, interactive effects on community dynamics (Zhu et al. 2016; Collins et al. 2022; Komatsu et al. 2019; Song, Hautier, and Wang 2023). For example, increased nutrient loading in grassland communities tends to decrease species richness and shift dominance structures (Stevens et al. 2004; Borer et al. 2017; Tilman 1985), where intensive soil disturbance can further impact diversity and stability depending on nutrient availability (Seabloom, Borer, and Tilman 2020). While the independent and interactive effects of global change drivers on ecological diversity and stability have been well-explored in some ecosystems (Tilman 1985; Komatsu et al. 2019; Avolio et al. 2021), the effects of multiple interacting drivers on temporal community dynamics, such as community synchrony, are less understood, particularly when contrasting short-term effects to those observed over long timescales (Valencia et al. 2020a; Ebel et al. 2022). Community synchrony quantifies correlations in temporal fluctuations in species' abundances (Loreau and de Mazancourt 2013); it depends on species interactions and responses to environmental conditions, and thus is likely strongly impacted by global change drivers (Hautier et al. 2020; Xu et al. 2022; Ebel et al. 2022). Studies with experimental manipulations of global change drivers and long-term data that capture transient versus post-transient trends in synchrony and stability are key for disentangling global change effects on community dynamics, validating theory and improving predictive power.

Long-term temporal patterns, such as changes in community synchrony, play critical roles in predicting global change effects on ecosystem dynamics, such as stability (Hautier et al. 2020; Ebel et al. 2022). Synchrony is inversely related to ecosystem stability, the degree of temporal fluctuations in total community biomass (Gonzalez and Loreau 2009; Loreau and de Mazancourt 2013; Thibaut and Connolly 2013). Highly synchronous dynamics can arise from shared responses to environmental fluctuations, thereby decreasing ecosystem stability (Tilman and Downing 1994; Ives, Gross, and Klug 1999; Valencia et al. 2020a). Conversely, compensatory dynamics define the tendency for periods of decreased abundance of some species to be offset by increased abundance in other species and are often driven by strong competition or opposing responses to environmental fluctuations, which increases stability (Ives, Gross, and Klug 1999; Yachi and Loreau 1999; Loreau and de Mazancourt 2013). Theory predicts that shifts in species richness alter temporal stability via changes in synchrony. For example, increased species richness is hypothesised to decrease synchrony and stabilise communities via the portfolio effect (Doak 1998; Tilman 1998), whereby more species stabilise aggregate community properties due to a statistical averaging effect. This relationship highlights the need to better understand the interactive effects of synchrony, stability, richness and evenness—especially in ecosystems impacted by global change.

Since the interactive effects of multiple global change drivers may arise over a decade after treatment (Komatsu et al. 2019), temporal community properties such as synchrony must be examined over multiple timescales. 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 that allow for comparisons of dynamics in the short- and long-term. Further, it is imperative to examine both independent and interactive effects of multiple global change drivers as certain drivers, such as pulse disturbances (e.g., drought, fire or tilling), can co-occur with ongoing press disturbances (e.g., atmospheric nitrogen deposition and warming). For example, long-term experiments show that disturbance may impact community composition during transient periods (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). Previous studies show conflicting relationships between global change drivers, 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, Yu, and Grogan 2023). These conflicting results may stem from differences in the time spans of studies, as community relationships shift through time and new effects appear late in succession.

Understanding synchrony and stability in grasslands in particular 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 run-off and atmospheric nitrogen deposition (Gruber and Galloway 2008). Here, we examine how two global change drivers—nutrient addition coupled with soil disturbance—impact grassland community synchrony, stability, richness and evenness across successional timescales. We use data from a 22-year grassland experiment at the Cedar Creek Ecosystem Reserve in Minnesota, given the site's history of studying stability and global change dynamics. Specifically, we build on previous work from Cedar Creek showing changes in species richness and community composition under disturbance and nitrogen addition (Seabloom, Borer, and Tilman 2020) and that the system recovered to novel, nutrient-mediated equilibria after approximately a decade of transient dynamics (DeSiervo et al. 2023). We ask the following: (1) How do disturbance and nitrogen addition alter community synchrony and stability? (2) How does diversity mediate the impacts of disturbance and nitrogen addition on synchrony–stability relationships? And (3) how do relationships between diversity, synchrony and stability change through succession? We hypothesised that disturbance would increase community synchrony (Table S1, H6; Lepš et al. 2019), but nitrogen addition may either increase or decrease synchrony (Table S1, H2; Gonzalez and Loreau 2009), dependent on changes in species interactions. Nitrogen addition and soil disturbance were expected to decrease stability (Table S1, H1, H5; Hautier et al. 2014; Connell and Slatyer 1977) by increasing biomass in favourable years of growth (Lee et al. 2010), leading to larger booms and busts in total biomass. We also expected that decreased richness due to nitrogen addition and disturbance (Seabloom, Borer, and Tilman 2020) would decrease stability due to portfolio loss (Lehman and Tilman 2000; Loreau et al. 2021; Doak 1998). Lastly, we hypothesised that synchrony will increase later in succession with nitrogen addition, as community dynamics are driven by a few dominant species under high nitrogen levels (Table S1, H2; Gonzalez and Loreau 2009). Furthermore, with increasing time since soil disturbance, stability would likely recover to predisturbance levels (Table S1, H5; Seabloom, Borer, and Tilman 2020).

2 | Materials and Methods

2.1 | Study Site and Data Collection

We analysed patterns in 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 across the 22 years was 6.7°C (± 0.02 SE), and precipitation was 818 mm (± 35 SE).

We briefly describe the experiment, with additional details in Tilman (1987) and Seabloom, Borer, and Tilman (2020). In 1982, identical nutrient addition experiments were established within two grids (35 × 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 tilled to remove vegetation and restart succession in the spring of 1982 (E002; Tilman 2021a). Each grid was split into 54 vegetation plots (4 × 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 0 N with 0 additional nutrients (μ), 0 N plus μ, and seven levels of nitrogen addition plus μ: 1.0, 2.0, 3.4, 5.4, 9.5, 17.0 and 27.2 $\mathrm{g\,N\,m^{-2}\,year^{-1}}$. Nitrogen was added annually as NH_4NO_3, and additional nutrients (μ) consisted of P, K, Ca, Mg, S and citrate-chelated trace metals (Supporting Information). We used the $0\,\mathrm{g\,N} + \mu\,\mathrm{m^{-2}\,year^{-1}}$ as our control for analyses to hold the inclusion of additional nutrients constant (see Supporting Information, Comparison of Control Conditions).

Above-ground biomass was clipped annually in a 10 × 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 intact sampled), 2001 (only intact sampled) and 2003 (only intact sampled in Fields A and B and only disturbed sampled in Field C). Starting in 1992, 81 plots were assigned to various nutrient cessation or burning treatments, and therefore excluded from the analyses. After further excluding 27 control plots without additional nutrients, we analysed a total of 216 plots. After 2004, experimental burning was expanded, and fence removal treatments were applied to all fields, limiting our time series to 1982–2004. We analysed species level and aggregated community biomass, removing woody species except for low-lying shrubs (see Supporting Information, Data Cleaning). Finally, we visualised temporal biomass trends for the most abundant species of six functional groups (C4 grasses, C3 grasses, annual and perennial nonleguminous forbs, legumes and low-lying shrubs) in intact and disturbed treatments under control ($0\,\mathrm{g\,N} + \mu\,\mathrm{m^{-2}\,year^{-1}}$) and high nitrogen addition ($27.2\,\mathrm{g\,N\,m^{-2}\,year^{-1}}$).

2.2 | Analysing Synchrony and Stability

We first investigated the relationships between synchrony and stability, respectively, with 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; Houlahan et al. 2007; Hallett et al. 2014; Loreau and de Mazancourt 2008). The variance ratio is determined as:

$$VR = \frac{\mathrm{var}(C(t))}{\Sigma_{i=1}^{N}\mathrm{var}\left(P_i(t)\right)} \tag{1}$$

where $P_i(t)$ is the above-ground biomass of species $i = 1, \ldots, N$, variances are calculated over time $t = 1, \ldots, T$, and $\mathrm{var}(C(t)) = \Sigma_{i=1}^{N}\mathrm{var}\left(P_i(t)\right) + 2\Sigma_{i=1}^{N-1}\Sigma_{j=i+1}^{N}\mathrm{cov}\left(P_i(t), P_j(t)\right)$. 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):

$$CV^{-1} = \frac{\mu}{\sigma} \tag{2}$$

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), comparing linear versus quadratic fits across the nitrogen gradient using the Akaike Information Criterion (AIC). Predictor variables included nitrogen (log-transformed to account for the geometric design of fertiliser amounts, continuous), disturbance (categorical) and the interaction between nitrogen and disturbance. We included field (categorical) as a fixed effect and grid (categorical) as a random effect in all models. Contrasts were calculated using emmeans (Lenth 2023).

To better understand global change effects on synchrony and stability, we decomposed the variance ratio (Equation (1)) and inverse coefficient of variation (Equation (2)). For synchrony, we compared how treatments affected changes in community variability, $\mathrm{var}(C(t))$, to changes in aggregate population variability, $\Sigma_{i}^{N}\mathrm{var}\left(P_i(t)\right)$. 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 log-transformed nitrogen addition, disturbance and their interaction, modelling field as a fixed effect and grid as a random effect, as above.

2.3 | Successional Dynamics

To determine the transient effects of global change drivers directly following the pulse soil disturbance and initiation of nutrient applications versus over a decade later, when communities settled on post-transient dynamical-equilibria, we subdivided our time series into a transient period from 1982 to 1988 and a post-transient period from 1993 to 2004, based on results from DeSiervo et al. (2023). We chose time windows encompassing 7 years of data to facilitate cross-period comparison while having long enough time series to obtain robust 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. Results are robust to different time series windows (e.g., 7 versus 10-years, Figure S4). We first fit separate linear models for each combination of nitrogen, disturbance treatment and successional period to visualise patterns in the synchrony–stability relationship.

Species diversity also influences synchrony and stability (Tilman 1987; Doak 1998), motivating us to examine the effects of nitrogen addition and disturbance on species richness, evenness, synchrony and stability using structural equation models (SEM). We calculated species richness by determining the maximum number of species censused annually in each plot and averaging per-plot richness across years, for the transient and post-transient phases, respectively. Similarly, we calculated average plot-level species evenness for each time period and plot using the E_{var} metric, which is independent of richness (Smith and Wilson 1996; See Supporting Information, E_{var} Metric).

We constructed a SEM for transient and post-transient periods to examine multidimensional community relationships, and compare how the strength of pathways changed during succession. We incorporated disturbance as a grouping variable into each SEM, resulting in separate models per disturbance treatment. Each endogenous variable was examined for normality, and we applied Box–Cox transformations to non-normal data. For each period, we evaluated each pathway's strength and sign using standardised path coefficients, which represent hypothesised causal relationships. Each SEM included a direct pathway from nitrogen addition to species richness, evenness, synchrony and stability. We also included pathways from species richness and evenness to synchrony and stability and from species richness to evenness. We built an initial, fully saturated SEM for both successional phases that contained all of our hypothesised relationships (Figure S6; Table S1), then removed all nonsignificant relationships. Model fits were determined using the chi-squared test. All SEMs were fitted and indirect effects calculated using the lavaan (Rosseel 2012).

To assess the effects of disturbance on model fit, we constructed additional SEMs where we constrained the effects of disturbance across all intact and disturbed plots to be identical, thus eliminating disturbance effects within each period. As above, we removed insignificant pathways. We compared these models with the above SEMs without constrained effects using AIC. We additionally constructed a SEM for the full time series (Figure S5).

3 | Results

3.1 | Full Time Series

Across the 22-year time series, the majority of communities were compensatory (VR <1), which was accentuated by soil disturbance and nitrogen addition (Figure 1A; linear model AIC $=-3.75$, quadratic model AIC $=9.06$; Table S3). At low nitrogen, disturbed plots were more compensatory than intact plots. However, synchrony in intact plots decreased with increasing nitrogen addition, causing synchrony across disturbance regimes to converge at high nitrogen levels (effect of nitrogen addition: $\widehat{\beta}=0.07\pm0.02$, $F_{1,208}=11.72$, $p<0.01$; effect of soil disturbance: $\widehat{\beta}=0.26\pm0.06$, $F_{1,208}=22.04$, $p=0.04$; interactive effect: $\widehat{\beta}=0.07\pm0.03$, $F_{1,208}=5.10$, $p=0.02$; Figure 1A; Table S2). Without nitrogen addition, soil disturbance decreased synchrony by 0.26 ± 0.06 on average (contrasts in synchrony: $t_2=4.38$, $p=0.05$). In contrast, synchrony in disturbed plots receiving the highest nitrogen treatment ($27.2\,\mathrm{g\,N\,m^{-2}\,year^{-1}}$) did not significantly differ from intact plots (contrasts in synchrony: $=0.04\pm0.06$, $t_2=0.04$, $p=0.58$). These compensatory temporal dynamics can be qualitatively observed via the opposing trends exhibited by two dominant species, C3 grasses *Agropyron repens* and *Poa pratensis*, especially under high nitrogen levels (Figure 3).

Nitrogen addition increased compensation by affecting aggregate population variability more so than community variability across disturbance regimes. While nitrogen addition increased community variability (Figure 1B; effect of nitrogen addition: $\widehat{\beta}=0.03\pm0.005$, $F_{1,236}=42.56$, $p<0.01$, Tables S8, S9), it had a stronger effect on population variability (Figure 1B; effect of nitrogen addition: $\widehat{\beta}=0.07\pm0.006$, $F_{1,236}=143.33$, $p<0.01$, Tables S6, S7). The effect of soil disturbance on population and community variability was also positive and of a similar magnitude, but with greater uncertainty (effect on population variability: $\widehat{\beta}=0.07\pm0.03$, $F_{1,2}=5.77$, $p=0.14$; effect on community variability $\widehat{\beta}=0.04\pm0.03$, $F_{1,2}=1.69$, $p=0.32$).

Stability decreased with increased nitrogen concentration and disturbance did not significantly alter the relationship between nitrogen and stability (Figure 2A, linear model AIC $=368.9$, quadratic model AIC $=375.9$; Tables S4, S5). Nitrogen addition decreased stability by 0.25 ± 0.04 on average ($F_{1,208}=49.6$, $p<0.01$), and disturbance had minimal impact on stability (main effect: $\widehat{\beta}=-0.03\pm0.17$, $F_{1,2}=0.15$, $p=0.73$, interaction; $\widehat{\beta}=0.05\pm0.07$, $F_{1,208}=0.42$, $p=0.52$). The mean and standard deviation of community biomass changed similarly with nitrogen addition over low-to-moderate nitrogen levels (0.0–$9.5\,\mathrm{g\,N\,m^{-2}\,year^{-1}}$), maintaining stability close to control levels (Figure 2B, points fall along the black reference line). However, at the two highest nitrogen levels, regardless of disturbance regime, communities deviated from the control, with increases in both mean and variability in total biomass (Figure 2B; Tables S12, S13, S10, S11). This decrease in biomass stability can also be qualitatively observed in temporal trends

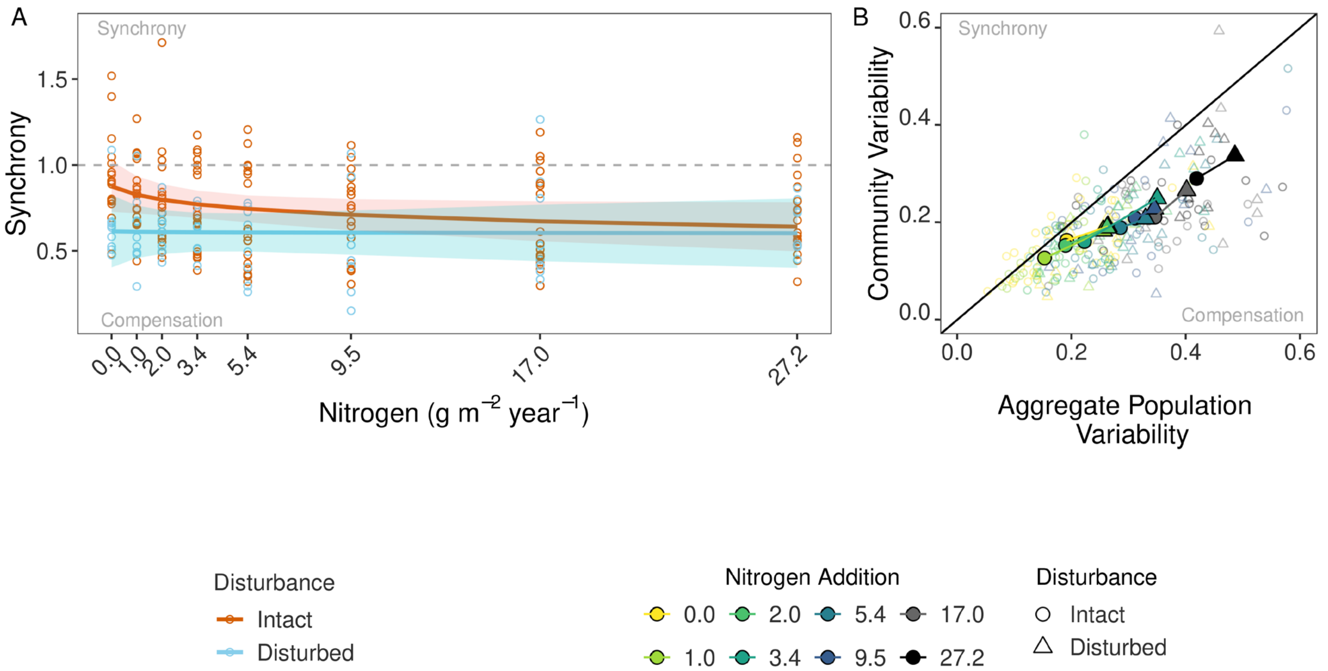

FIGURE 1 | Synchrony and its two components across global change treatments. (A) shows synchrony in intact plots decreases across the nitrogen gradient until communities converge with disturbed plots at high nitrogen levels. The dotted line represents a variance ratio (VR) of 1, which indicates the transition from synchronous (VR >1) to compensatory (VR <1) dynamics. Best fit lines are averaged across field using emmeans (Lenth 2023). Model summaries can be found in Tables, S2, and S3. (B) shows that most communities are compensatory because of a greater increase in aggregated population variability (denominator in Equation (1)) than in community variability (numerator in Equation (1)). The filled-in circles and triangles represent the mean per treatment, while faint circles and triangles show raw data. If populations fluctuate independently through time, points will fall along the black 1:1 line. The area above the line denotes synchronous dynamics while the area below the line denotes compensatory dynamics.

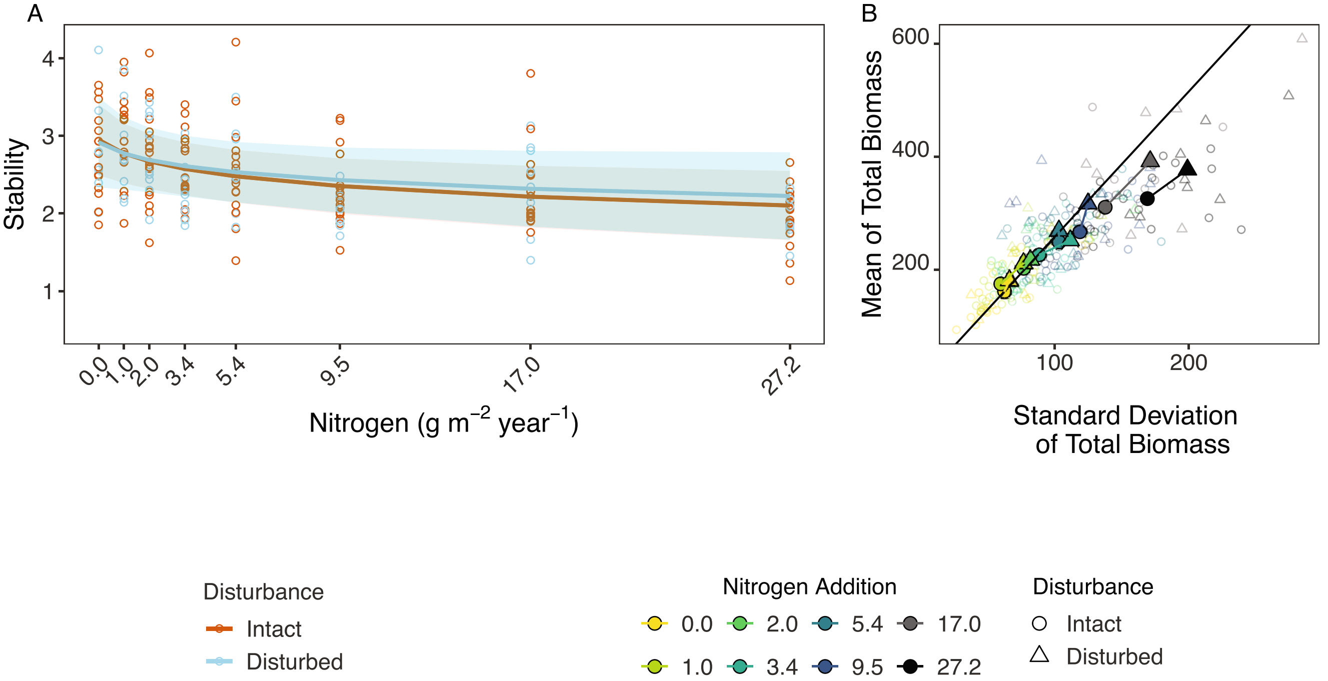

FIGURE 2 | Stability and its two components across global change treatments. (A) shows that stability has a negative relationship with increasing nitrogen concentration across disturbance regimes. Best fit lines are averaged across field using emmeans (Lenth 2023). Model summaries can be found in Tables, S4, S5. (B) shows that at high nitrogen levels, communities begin to deviate from the control with stronger relative increases in the standard deviation in total biomass. The filled-in circles and triangles represent the mean per treatment, while faint circles and triangles show raw data. The black line denotes the stability of the control plot (i.e., no disturbance, $0\,\mathrm{N}+\mu$), with the area above showing increased stability compared to the control and the area below showing decreased stability.

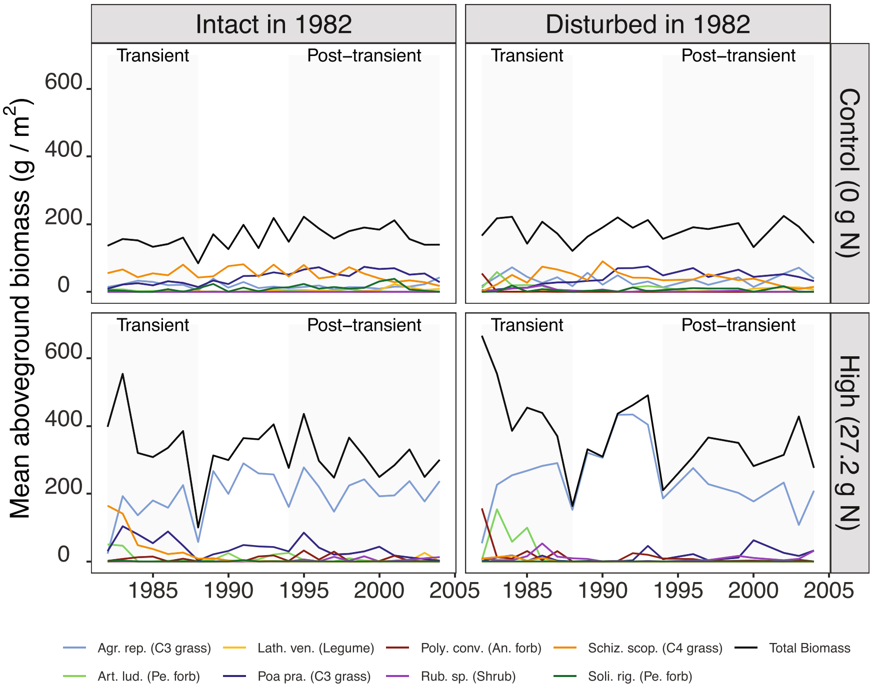

FIGURE 3 | Average total above-ground biomass (black line) and biomass of the top one or two most abundant species from different functional groups (coloured lines) in control plots (0 g N m^{-2} year^{-1} + μ) and fertilised plots (27.2 g N m^{-2} year^{-1} + μ) and intact (left) and disturbed plots (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 Figures 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.

of total community biomass, with increased community mean biomass coupled with more variability through time in fertilised plots (Figure 3 black total biomass line).

3.2 | Successional Dynamics

While the synchrony–stability relationship was overall negative, the strength of the relationship depended on the interplay between disturbance, nitrogen addition and time period (Figure 4). In intact plots, the synchrony–stability relationship remained similar across time and nitrogen treatment (Figure S2). In comparison, during both the transient and post-transient time periods, disturbance and nitrogen weakened this relationship (i.e., less negative slopes at moderate and high nitrogen levels in disturbed plots; Figure 4), motivating us to disentangle dynamics across time periods and global change drivers.

The SEMs confirmed that the effect of nitrogen addition differed between the two successional periods and that soil disturbance changed several community relationships across time (Figure 5, Tables S14, S15). During the transient phase, nitrogen addition decreased synchrony in plots that did not experience disturbance (standardised path coefficient of -0.30 ± 0.07, $p < 0.01$) but increased synchrony in plots that were disturbed (0.31 ± 0.16, $p = 0.05$). In contrast, during the post-transient phase, nitrogen had a weakly positive effect on synchrony in intact plots (0.17 ± 0.08, $p < 0.02$), but no effect on synchrony in disturbed plots.

Nitrogen addition and disturbance also differentially affected community stability. In the transient phase, nitrogen decreased stability in the absence of disturbance (-0.35 ± 0.07, $p < 0.01$; Figure 5A) and had no effect on disturbed plots (Figure 5C). In the post-transient phase, nitrogen maintained strong negative effects on stability in intact plots (-0.29 ± 0.05, $p < 0.01$; Figure 5B), but also developed strong negative effects in disturbed plots (-0.36 ± 0.07, $p < 0.01$; Figure 5D). Indirect effects arose along the pathways between nitrogen, synchrony and stability, where synchrony mediated nitrogen's effect on stability in both intact and disturbed plots. In intact plots, we found a positive mediation effect of synchrony between nitrogen and stability during the transient phase (indirect path coefficient of 0.18 ± 0.001, $p < 0.01$), but this mediation effect was negative in the post-transient phase (indirect path coefficient of -0.10 ± 0.002, $p = 0.03$). However, synchrony was not a significant mediator of the nitrogen–stability relationship in disturbed plots, regardless of successional phases.

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 and disturbance treatments (transient, intact: -0.69 ± 0.04, $p < 0.01$; transient, disturbed: -0.59 ± 0.04, $p < 0.01$; post-transient, intact: -0.55 ± 0.04, $p < 0.01$; post-transient, disturbed: -0.48 ± 0.04, $p < 0.01$; Figure 5). The effect of nitrogen addition on species evenness increased through time in intact plots but was maintained in disturbed plots (transient, intact: no pathway;

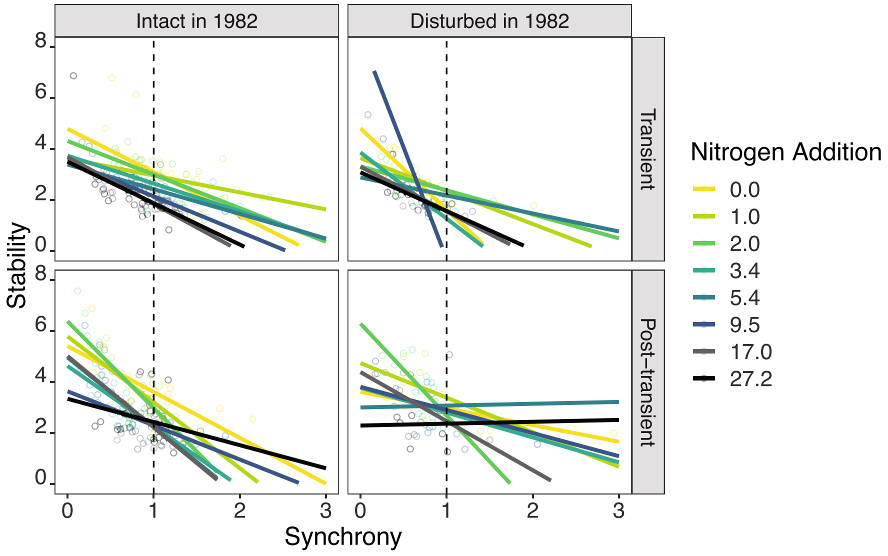

FIGURE 4 | Synchrony and temporal stability across communities over the 22-year time series, dependent on nitrogen addition (colours), disturbance treatments (columns), and successional phase (rows). The dotted, vertical line represents independent fluctuations (VR = 1), separating compensatory (left 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 variable relationship, especially in disturbed plots).

transient, disturbed: −0.41 ± 0.09, $p < 0.01$; post-transient, intact: −0.66 ± 0.07, $p < 0.01$; post-transient, disturbed: −0.29 ± 0.13, $p = 0.03$), becoming as strong as the effect on species richness during the post-transient period in intact plots particularly. As with synchrony, species richness mediated the relationship between nitrogen and stability; however, it only had an important effect during the transient phase. In intact transient plots, species richness had a negative indirect effect (indirect path coefficient of −0.17 ± 0.001, $p < 0.01$), which was strengthened in disturbed plots (indirect path coefficient of −0.30 ± 0.002, $p < 0.01$).

Community diversity and synchrony affected community stability differently across both successional phases and disturbance treatments (Figure 5). Initially, species richness and evenness had significant impacts on stability in the transient phase, though evenness only affected stability in disturbed plots (−0.15 ± 0.07, $p = 0.03$). Richness had strong positive effects on stability, particularly in disturbed plots (intact: 0.25 ± 0.07, $p < 0.01$; disturbed: 0.51 ± 0.19, $p < 0.01$; Figure 5C). However, the effects of diversity diminished in the post-transient phase, resulting in insignificant effects of richness and evenness on stability. In contrast, the effects of synchrony on stability were strong and persistent across disturbance treatments, though we observed a moderate decrease in the magnitude of their relationship after transience, especially in plots that experienced soil disturbance (transient, intact: −0.60 ± 0.05, $p < 0.01$; transient, disturbed: −0.87 ± 0.06, $p < 0.01$; post-transient, intact: −0.58 ± 0.05, $p < 0.01$; post-transient, disturbed: −0.50 ± 0.07, $p < 0.01$).

Structural equation models were well-supported by data grouped by disturbance treatment and split between a transient and post-transient period (transient $p = 0.74$, $df = 8$; post-transient $p = 0.76$, $df = 9$). Models without disturbance effects, achieved by constraining parameters to be equal across disturbance treatments, were poorly fitting (transient $p < 0.01$, $df = 21$; post-transient $p = 0.04$, $df = 23$). Models including disturbance were also supported via AIC (transient, nonconstrained AIC = 833.00, transient, constrained AIC = 930.18; post-transient, nonconstrained AIC = 578.80, post-transient, constrained AIC = 581.09). Likewise, modelling the full time series without defining separate phases of succession resulted in poorly fitting models ($p < 0.01$, $df = 9$; Figure S5).

4 | Discussion

There is ample evidence suggesting global change decreases community stability (Zhang et al. 2018; Ma et al. 2017; Xu et al. 2022; Hautier et al. 2015; Song, Hautier, and Wang 2023), but the effects of global change drivers on community synchrony are less documented. Our analysis of long-term data demonstrated that, across successional timescales, communities tend towards compensation in response to nitrogen addition and soil disturbance (Figure 1A). Both drivers lowered community synchrony by increasing aggregated population variability more than community variability (Figure 1B). This is likely because soil disturbance restarted succession, inducing compensatory dynamics as community composition experienced high turnover (Gonzalez and Loreau 2009; Seabloom, Borer, and Tilman 2020; DeSiervo et al. 2023). Nitrogen addition further benefited dominant species, driving large increases in population variability due to strong competition, especially at high nitrogen levels (Clark and Tilman 2008; Isbell et al. 2013; Seabloom, Borer, and Tilman 2020). Despite the stabilising potential of compensatory dynamics, nitrogen addition also decreased community stability, weakening the strong negative relationship between synchrony and stability, especially in disturbed communities experiencing high nitrogen inputs (Figures 2B, 4). Thus, nitrogen addition induced a shift towards more compensatory but less stable communities, possibly driven by reductions in species richness that weakened portfolio effects, and benefited only a few dominant

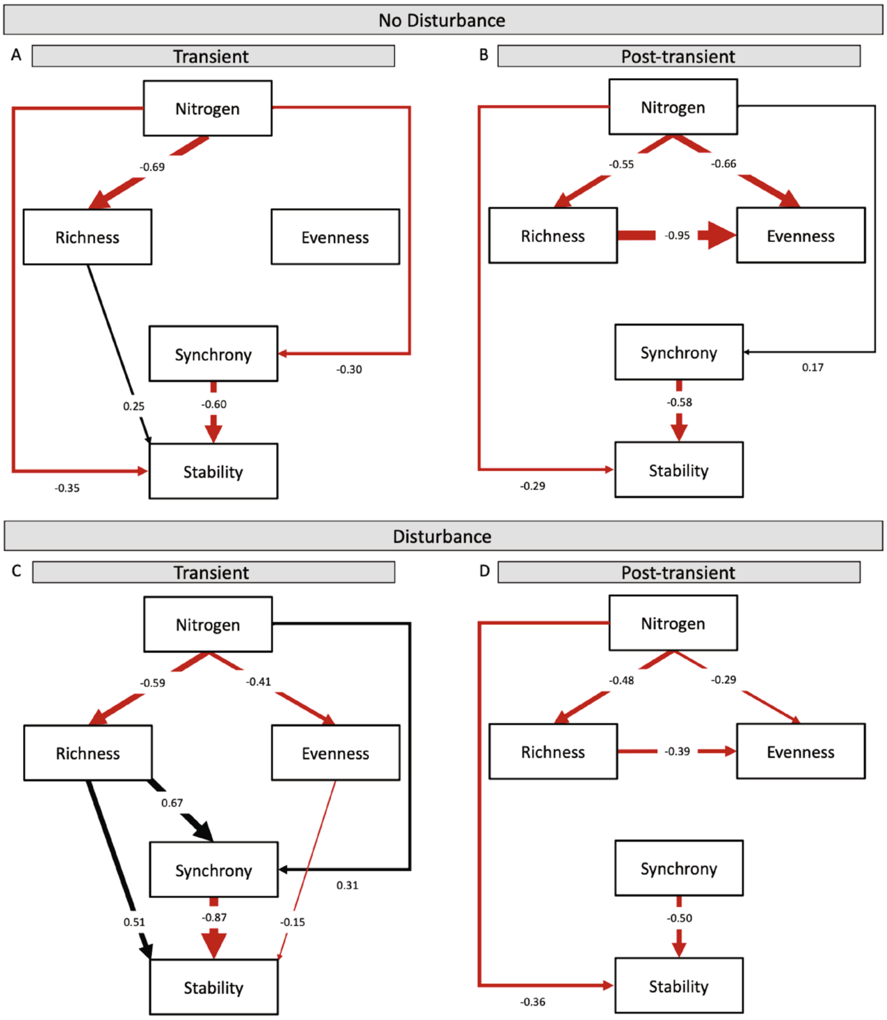

FIGURE 5 | Path diagrams of the structural equation models displaying shifting relationships among global change drivers, biodiversity, synchrony and stability. Models were fit to data collected during the transient phase (1982–1988) in intact (A) and disturbed (C) plots, and after the transient phase (1994, 1996–1997, 1999–2000, 2002–2004) in intact (B) and disturbed (D) plots. Both SEMs are well-fitting (transient: $p = 0.74$, $df = 8$; post-transient: $p = 0.76$, $df = 9$; n intact plots = 144, n disturbed plots = 72). Values next to each arrow indicate the standardised coefficient of the direct effect. Red arrows indicate negative relationships, while black arrows indicate positive relationships. The widths of the arrows are proportional to the magnitude of each relationship. Summaries of direct effects can be found in Tables S14 and S15.

species. This result signifies that expected relationships between synchrony and stability are dynamic and that these well-established links cannot always reliably predict the effects of global change on communities if they themselves are vulnerable to change. Additionally, our results highlight that overall community responses to global change emerge and interact at differing temporal scales, requiring long-term data to disentangle.

While synchrony decreased with nitrogen addition and disturbance, our investigation found that community stability decreased as well—contradicting theoretical synchrony–stability relationships, but matching the previous literature and our hypotheses (Table S1, H1, H5). Although fertilisation yielded an increase in mean annual biomass, this did not enhance stability (i.e., the overyielding effect; De Mazancourt et al. 2013). Rather, nitrogen addition also increased the temporal variability of total biomass, resulting in large booms and busts, and an overall decrease in stability (Hautier et al. 2014, 2020; Carroll et al. 2022; Seabloom et al. 2021). Surprisingly, soil disturbance did not lead to a further reduction in stability, as anticipated given previous findings that grassland stability declines with an increasing number of global change drivers (Song, Hautier, and Wang 2023). Instead, stability remained similar across disturbance regimes (Figure 2A; Seabloom, Borer, and Tilman 2020). Although these results align with expectations from global change ecology, they are surprising considering our findings on synchrony, as increased compensation often indicates greater stability.

While our full time series results indicate that both synchrony and stability decrease with global change drivers, theory suggests and previous empirical results support a strong negative synchrony–stability relationship, as observed during the transient period of succession (Figures 4, 5; Valencia et al. 2020a). Through evaluating the indirect nitrogen–synchrony–stability pathway in intact plots, we also find a moderate positive effect of nitrogen on stability when mediated by synchrony, affirming the theoretical prediction that any driver that decreases synchrony, as nitrogen does, should therefore increase stability. However, the direct negative effect of nitrogen addition on community stability was stronger than this positive indirect effect, reinforcing previous findings that nutrient addition will generally destabilise communities (Yang et al. 2022; Carroll et al. 2022; Bharath et al. 2020). Additionally, nitrogen did not impact stability in transient, disturbed plots (Figure 5C), though it strongly decreased stability in intact plots (Figure 5A). This discrepancy could be attributed to nitrogen addition having an immediate effect on intact grasslands, inducing greater variability in biomass among present species at high nitrogen concentrations (Figure 2B). Meanwhile, in disturbed plots, there may have been a lag in the manifestation of nitrogen effects on stability (Figure 3); without strong competition from other species, nitrogen-benefiting pioneer species could have taken advantage of priority effects, minimising variability in community growth and total biomass during transience.

Community stability was only affected by biodiversity in the transient period (Figure 5A,C). Species richness in particular had strong positive effects on stability; when the nitrogen stability pathway was mediated by richness, we found that nitrogen's negative effect was dampened. These findings support 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 destabilise 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, Borer, and Tilman 2020; Hautier et al. 2020). However, we only found evidence of the portfolio effect during the transient period, suggesting that biodiversity is most important when communities are reassembling after disturbance, and has a lesser impact on mitigating global change effects once the community has reached a steady state post-transience.

Although the direct synchrony–stability relationship was still strongly negative post-transience, the magnitude of the relationship decreased over time. This was particularly true in plots that experienced soil disturbance, where this relationship initially emerged strongly but tapered off post-transience (Figure 5C,D). This result runs counter to theory, where we would have expected a persistently strong inverse relationship between the two dynamics, but instead, the relationship effectively decoupled at high nitrogen levels in disturbed plots (Figures 4, 5D). Following experimental treatments, a strong increase in plant community biomass (Figure 3) was sustained by consistent nitrogen addition in fertilised plots (Tilman 1987; Inouye and Tilman 1988). Therefore, the weakened relationship emerged in the post-transient phase due to continuous nitrogen input sustaining high plant biomass while also promoting instability, showcasing how global change drivers maintained lagged effects on synchrony and stability dynamics.

Several relationships between global change, biodiversity and community dynamics shifted, disappeared or materialised post-transience. The overall effect of soil disturbance on all community properties lessened through time, yielding no significant differences between intact and disturbed plots in the later stages of succession (Figure 5B,D). Similarly, the effects of biodiversity on both synchrony and stability dynamics also decreased post-transience (Figure 5B,D). This transition to insignificant effects further highlights the importance of biodiversity in bolstering stability in the transient years following global change impacts, while revealing that it may not play as strong a role post-transience, once the communities have reached new equilibria (DeSiervo et al. 2023). However, as communities approached these new equilibria, a strong negative relationship between richness and evenness emerged post-transience (Figure 5B,D). This is likely because, after the transient phase, nitrogen addition forced a dominance structure that favoured a few species (Tilman 1990), reducing evenness over time. Overall, we found that global change drivers had varying effects on community parameters across time and disrupted pre-established notions on dynamic relationships, challenging our preconceptions on how synchrony, stability and biodiversity are expected to respond to anthropogenic impacts over long timescales. By examining the multidimensional impacts of global change drivers on community dynamics, we found that nitrogen addition and soil disturbance decreased synchrony and stability, altering the magnitude and direction of diversity–stability relationships over time. The generality of these changes, and the timescales at which they arise, will likely depend on species traits and environmental variability. For example, we expect annually dominated systems to show quicker responses and greater synchrony after global changes compared with perennially dominated systems (Shoemaker et al. 2022; Werner, Young, and Stuble 2024). Critically, we find that dynamics, such as the role of diversity in mediating synchrony and stability, change over time, necessitating further scrutiny of how these patterns yield different community responses to global change drivers. Long-term data are particularly important for studying synchrony, as analysing short time series may result in erroneous conclusions that bias results towards showing more synchronous than compensatory dynamics (Valencia et al. 2020b; Luo et al. 2021). Our results align with research from grassland systems across multiple continents, where global change drivers have restructured community compositions and competitive hierarchies (Avolio et al. 2021), affecting ecosystem productivity even in cases where species richness was maintained (Komatsu et al. 2019; Avolio et al. 2014). Incorporating synchrony into future research on the long-term impacts of global change drivers is crucial for understanding the direct and indirect mechanisms by which global change affects community dynamics and ecosystem stability.

Author Contributions

J.L.D. and K.R.M. contributed equally and are co-first authors. M.H.D. and L.G.S. contributed equally and are co-last authors. J.L.D., K.R.M., M.H.D. and L.G.S. conceived the idea for the study. J.L.D. and K.R.M. performed model analyses, with significant contributions from M.S., D.G., N.I.W., C.M.W., M.H.D. and L.G.S. J.L.D., K.R.M., M.S., D.G., N.I.W., M.H.D. and L.G.S. contributed to writing the first draft of the manuscript, and all authors contributed to revisions.

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Data Availability Statement

Data and code are archived on Zenodo at https://doi.org/10.5281/zenodo.13921433.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.