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LETTER

Disturbance alters transience but nutrients determine equilibria during grassland succession with multiple global change drivers

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Abstract

Disturbance and environmental change may cause communities to converge on a steady state, diverge towards multiple alternative states or remain in long-term transience. Yet, empirical investigations of successional trajectories are rare, especially in systems experiencing multiple concurrent anthropogenic drivers of change. We examined succession in old field grassland communities subjected to disturbance and nitrogen fertilization using data from a long-term (22-year) experiment. Regardless of initial disturbance, after a decade communities converged on steady states largely determined by resource availability, where species turnover declined as communities approached dynamic equilibria. Species favoured by the disturbance were those that eventually came to dominate the highly fertilized plots. Furthermore, disturbance made successional pathways more direct revealing an important interaction effect between nutrients and disturbance as drivers of community change. Our results underscore the dynamical nature of grassland and old field succession, demonstrating how community properties such as β diversity change through transient and equilibrium states.

KEYWORDS
community assembly, community trajectory analysis (CTA), disturbance, eutrophication, fertilization, old fields, succession

INTRODUCTION

Temporal change in ecological communities has long fascinated ecologists, prompting a rich study of succession that underpins many theories in community ecology (Chang et al., 2019; Clements, 1916; Gleason, 1926; Pickett et al., 2009). In the modern era of rapid environmental change, ecological disturbances and temporal dynamics are now interacting with multiple global change drivers known to influence community composition and structure (Chang et al., 2019). Consequently, there is a renewed interest in updating our understanding of succession through data–theory integration using contemporary approaches that capture the complex determinants of community composition change (Avolio et al., 2021). A recent metaanalysis of global change experiments in herbaceous plant communities determined that the effects of multiple global change drivers on communities were typically synergistic, but lagged, and often only detectable over long (≥10 years) timescales (Komatsu et al., 2019). Building on foundational theory of ecological succession and community assembly is essential for understanding community responses to anthropogenic drivers of change, and to improve conservation and restoration outcomes in a rapidly changing world (Chang et al., 2019; Komatsu et al., 2019).

Early models in successional theory predicted that communities change directionally over time towards a climax system (Clements, 1916; Lepš & Rejmánek, 1991; Pickett et al., 2009). Inherent in this historical paradigm of succession is convergence: a process where spatially segregated communities experiencing the same environmental conditions equilibrate to the same species composition and structure regardless of underlying spatiotemporal variability in starting conditions. The final stable state community, which persists in perpetuity until a disturbance restarts the successional process, consists of a suite of coexisting species with stable population dynamics (Law, 1999). Resource-based competition models of community structure (e.g. R* theory) predict that nutrient supply rate is the primary determinant of equilibrium plant community assemblages, assuming all species can reach all locations (Tilman, 1985; Tilman & Wedin, 1991; Wilson & Tilman, 1991, 1993) and that spatially segregated communities with the same nutrient supply will converge on similar species composition, regardless of disturbance or variable starting conditions (Inouye & Tilman, 1988). A change in nutrient supply, however, is predicted to shift the equilibrium community towards a new, possibly irreversible stable state (Suding et al., 2004). For example, in the grassland system, we focus on here, Isbell, Reich, et al. (2013) found that plant communities persisted in a low-diversity state more than two decades after the cessation of nutrients, suggesting that fertilization caused a regime shift.

Directly contradicting a predictable, resource-based competition paradigm of succession, more recent theory has emphasized how stochastic and heterogeneous factors including small-scale abiotic variation, probabilistic dispersal, colonization and local extinction can lead to divergent communities that exhibit alternative stable states (Fukami, 2015; Fukami & Nakajima, 2011; Miller et al., 2021; Shoemaker et al., 2020). Priority effects including niche pre-emption and modification from early arriving species can result in multiple, alternative steady-state pathways across locations that had different species arrival order, even under the same environmental conditions (Fukami, 2015). For example, Chase's mesocosm study (Chase, 2003) demonstrated that successional trajectories in aquatic mesocosms with intermediate productivity exhibited alternative stable states depending on the initial density of a single organism (snails). Evidence for alternative steady-state pathways also occurs in plant systems. For example, one empirical study examining patterns of plant succession after the eruption of Mt. St. Helens found evidence for multiple successional pathways within and among sites, which the authors attribute to the interaction of disturbance, spatial contingencies and other chance factors (Chang et al., 2019). Theoretical modelling suggests that divergence between communities is more likely to occur with a large species pool, low connectivity, high productivity and infrequent disturbance (Chase, 2003). In parallel, divergence can also depend on small-scale local heterogeneity (spatial contingencies) (Kardol et al., 2007; Young et al., 2017) and the environmental drivers experienced at a single point in time, especially early in succession (Werner et al., 2020).

Though many community theories focus on final equilibrium dynamics, it has long been recognized that real-world communities can persist for long periods without reaching an equilibrium (Cowles, 1899; DeAngelis & Waterhouse, 1987; Fukami & Nakajima, 2011; Hastings, 2004; Huston, 1979; Noy-Meir, 1975). In many cases of long-term transience, disturbance occurs frequently enough that species are consistently reshuffled and the community never reaches a point where composition is stable (Fukami, 2015; Huston, 1979). Even simple models of community assembly can produce prolonged transience when there is sufficient temporal variability. For example, a Lotka–Volterra competition model of a grassland system with periodic disturbance and seasonal changes led to sustained dynamic transience, where modelled species compositions shifted towards equilibria without enough time to reach the predicted state before shifting yet again (Geijzendorffer et al., 2011). Though several studies demonstrate dynamics that are consistent with long-term transience, few studies provide quantitative metrics, such as the rate of community turnover, to accurately identify transience. One exception is a recent study examining a long-term restoration project in the drylands of China, which demonstrated a prolonged period of transience of shrub dominance (around 37 years), followed by a rapid shift to the restored state characterized by low shrub cover and high grass cover (Chen et al., 2019).

Characterizing successional trajectories in practice necessitates high spatial and temporal replication that can capture the long-term behaviour of the system (Hastings, 2004, 2010; Inouye & Tilman, 1988). Thus, there are few experimental studies in plant communities with time series sufficiently long to capture asymptotic trends in community composition and to distinguish between competing theories of successional dynamics (Hastings, 2004, 2010). To address this knowledge gap, we analysed a long-term (22-year) experiment from the Cedar Creek Ecosystem Reserve in Minnesota, USA to examine community succession in three old fields experiencing two anthropogenic drivers of change: soil-tilling disturbance and nutrient addition. This is an ideal system to examine succession due to a long history of study at Cedar Creek (Isbell, Reich, et al., 2013; Tilman, 1987; Wilson & Tilman, 1991, 1993), including a rich natural history knowledge base of the common species in this system (Catford et al., 2019; Sullivan et al., 2018). We focus on the joint effects of both drivers, as both community response to nutrient supply (Isbell, Reich, et al., 2013; Tilman, 1987; Wilson & Tilman, 1991, 1993) and recovery from agricultural disturbance (Debussche et al., 1996; Holt et al., 1995; Isbell et al., 2019; Li et al., 2016; Nerlekar & Veldman, 2020; Pickett et al., 2009) have been well-studied individually, but their joint effects are less understood (Seabloom et al., 2020). If communities at Cedar Creek tend towards alternative stable states or prolonged transience, disturbance could alter the predictions from adding nutrients alone. An earlier short-term analysis of successional change from Cedar Creek found that species composition changed rapidly in response to nutrient addition, but that 4 years was insufficient to determine community convergence to resource-controlled equilibria versus divergence or long-term transience (Inouye & Tilman, 1988). A more recent analysis from Cedar

Creek suggests an interactive effect between nutrients and disturbance on species diversity and total biomass that emerges after a decade of recovery (Seabloom et al., 2020); however, this study did not evaluate the joint effects of nutrients and disturbance on community composition nor successional trajectories.

Here, we revisited Inouye and Tilman's initial investigation of succession (Inouye & Tilman, 1988), extending from their focus on convergence versus divergence to additionally ask: (1) Do communities tend towards equilibrium states, remain in long-term transience or reach alternative stable states? (2) Do soil resources determine long-term composition? and (3) Are successional trajectories altered by disturbance? To address whether communities settled into a steady state, or persisted in long-term transience, we examined the rate of community compositional change between years, and the directionality of those changes. If communities progressed along a successional pathway towards a stable equilibrium (single or multiple equilibria), then we expected community turnover to decline, and community trajectories to display directionality in multivariate space as they move towards equilibria. To address whether nutrient addition led to the development of resource-controlled equilibria, or if disturbance or variable starting conditions yielded alternative stable states, we looked for evidence of convergence or divergence in composition between spatially segregated communities within and across experimental treatments and fields.

MATERIALS AND METHODS

Study site and data collection

Data were collected in successional grassland fields at the Cedar Creek Ecosystem Science Reserve in Minnesota, USA (CDR, Lat: 45.4 Long: 93.2 W) from 1982 to 2004. CDR has well-drained sandy soils that are low in nitrogen (N), resulting in low productivity relative to other grasslands worldwide (Fay et al., 2015). The mean annual temperature during experimentation from 1982 to 2004 was 6.7°C (±0.02 SE) and the mean annual precipitation was 818 mm (±35 SE). There were two consecutive notable drought years during the experiment (1987 and 1988) where annual precipitation was below 600 mm.

The experimental design is described briefly here, with additional details in Tilman (1987) and Seabloom et al. (2020). In 1982, identical disturbance × nutrient addition experiments were established in three abandoned agricultural fields within 5 km of one another that were last tilled and farmed in 1968 (Field A), 1957 (Field B) and 1934 (Field C). Field A and Field B were last planted with soybeans, while Field C was last planted with corn. Previous research at Cedar Creek suggests that soil N increases with time since agricultural abandonment (Inouye & Tilman, 1988; Tilman, 1987); consistent with that pattern, Field C had the highest soil N concentration ($638\,\mathrm{mg\,kg}^{-1}$) in 1982 before experimentation. Inconsistent with this pattern, Field B had the lowest soil N concentration ($377\,\mathrm{mg\,kg}^{-1}$) while Field A, the youngest field, was intermediate ($582\,\mathrm{mg\,kg}^{-1}$). Prior to the experiment, Field A was dominated by the C3 grass *Agropyron repens*, while both Field B and Field C were dominated by the C4 grass *Schizachyrium scoparium* and Field C also had some scattered *Quercus* seedlings, but no mature trees.

Within each of the three Fields, two grids (35 × 55 m) were established in 1982 for nutrient application, one in an area that was thoroughly disked in the spring of 1982 (E002), and another in an adjacent area that remained intact with old field vegetation (E001). The disking treatment pulverized the existing vegetation, leaving bare soil which was then raked to remove clumps of vegetation. Each grid consisted of 54, 4 × 4 m vegetation plots, receiving one of nine nutrient treatments (applied annually in May or June) in a randomized block design, with six replicate plots per field. Nitrogen was added as NH_4NO_3 and the micronutrients (μ) consisted of P, K, Ca, Mg, S and citrate-chelated trace metals (P_2O_5 at $20\ \mathrm{g} \cdot \mathrm{m}^2 \cdot \mathrm{year}^{-1}$, K_2O at $20\ \mathrm{g} \cdot \mathrm{m}^2 \cdot \mathrm{year}^{-1}$, $CaCO_3$ at $40\ \mathrm{g} \cdot \mathrm{m}^2 \cdot \mathrm{year}^{-1}$, $MgSO_4$ at $30\ \mathrm{g} \cdot \mathrm{m}^2 \cdot \mathrm{year}^{-1}$, $CuSO_4$ at $18\ \mu\mathrm{g} \cdot \mathrm{m}^2 \cdot \mathrm{year}^{-1}$, $ZnSO_4$ at $37.7\ \mu\mathrm{g} \cdot \mathrm{m}^2 \cdot \mathrm{year}^{-1}$, $CoCO_2$ at $15.3\ \mu\mathrm{g} \cdot \mathrm{m}^2 \cdot \mathrm{year}^{-1}$, $MnCl_2$ at $322.0\ \mu\mathrm{g} \cdot \mathrm{m}^2 \cdot \mathrm{year}^{-1}$ and $NaMoO_4$ at $15.1\ \mu\mathrm{g} \cdot \mathrm{m}^2 \cdot \mathrm{year}^{-1}$). Importantly, the soil disking (hereafter referred to as the disturbance treatment) occurred once at the beginning of the experiment, while the nutrient additions were applied annually throughout the experiment.

Though our emphasis is on the successional trajectories of the three old fields with the disturbance X nutrient treatments (Fields A, B and C), a nearby remnant grassland within a native oak savannah (Field D) that had never been clear-cut or ploughed was also surveyed annually and provides a comparison for our study. In 1982, Field D had a soil N concentration of $593\,\mathrm{mg\,kg}^{-1}$, (comparable with both Field A and Field C) and was dominated by *Carex* spp. After the first vegetation survey of plots in summer 1982, the vegetation composition of the intact grids of Field C and B most closely resembled the remnant Field D (Figure S1). In contrast, the composition of the intact grid of Field A was distinct from Field D, and all recently disturbed grids were distinct from Field D (Figure S1). After the first vegetation survey of plots in summer 1982, Field D had the highest species richness at 15.7 species per plot, followed by the unfertilized control plots in the intact grid of Field C, at 13.8 species per plot (Figure S2).

Beginning in 1982, vegetation was sampled by clipping a 10 X 300 cm strip each year within each plot at the ground level. After clipping, biomass was sorted into previous year's growth (litter), and current year's growth (live biomass). Live biomass was sorted by species, dried and weighed to the nearest 0.01 g. All plots in all fields were sampled annually with the exception of years 1995 (only E001 sampled), 2001 (only E001 sampled) and 2003 (only E001 and Field C E002 sampled). Due to new treatments (experimental burning and fence removal) among the three experimental fields after 2004, we restricted our analyses to the time period 1982–2004. Additionally, beginning in 1992, three randomly chosen replicate plots within each nutrient treatment in the E002 grid received nutrient cessation and experimental burning, which we excluded for our analyses from 1992 onwards. We conducted statistical analyses on plot-year combinations with original disturbance X nutrient treatments established in 1982. Prior to all multivariate analyses, we applied a $\ln(1+x)$ data transformation where $x =$ biomass (in g) of individual plant species within a plot in a given year.

Statistical analyses

Explained variability and overall trends in community composition

To assess how the disturbance event in 1982, yearly nutrient application and historical contingencies of each field explained community composition throughout the experiment, we used a Permutational ANOVA (PERMANOVA) using the *adonis* function from package *vegan* (Oksanen et al., 2008) in R version 4.1.2 (R Core Team, 2020) with the Bray–Curtis dissimilarity matrix generated from species' biomass data from all plots for each year from 1982 to 2004. The Bray–Curtis matrix of a given year was the dependent variable, with three additive independent variables: disturbance (categorical), nutrient treatment (continuous from 0 to 27.2 $\text{g}\cdot\text{m}^2\cdot\text{year}^{-1}$) and field (categorical). We included field as a fixed effect, as we were interested in how differences among fields from variable legacies of agricultural abandonment may explain differences in composition through time. We examined yearly trends in the explained variation (partial R^2) for each independent variable over the 22 years of the experiment in the PERMANOVA model, evaluating which variables explained the most variation in community composition, and the longevity of those effects.

To provide context for our multivariate results, we report trends in biomass, species richness and the relative proportion of plant functional groups across disturbance × nutrient treatments. To determine which plant species were driving variation in composition, we performed an indicator species analysis using the *multipatt* function from package *indicspecies* (De Caceres & Legendre, 2009) in R. Indicator species analyses assess the association between species patterns and combinations of groups of sites, and perform permutation tests for statistical significance of the best matching associations (De Caceres & Legendre, 2009). For the analysis, we grouped sites according to disturbance treatment (remnant field D, and grids E001 and E002), nutrient treatment (control and 27.2 $\text{g N}\cdot\text{m}^2\cdot\text{year}^{-1}$ plots only) and timing relative to the start of the experiment (early: 1982–1985, and late: 2000–2004). We constrained the analysis to include species associated with one to four of the aforementioned groups, and we report species with the highest group associations.

Assessing convergence versus divergence

To test if plots receiving the same disturbance X nutrient treatment converged or diverged in community composition over time (β diversity), we calculated the average Bray–Curtis distance of replicate communities within treatments to their nutrient group centroids using the *betadisper* function from the R package *vegan* (Oksanen et al., 2008). If the distance between plots to their group centroids declined over time, this indicated convergence (lower β diversity among plots within a treatment). We evaluated trends of the average distance to the centroid over the 22-year time series for each disturbance × nutrient treatment. One way to evaluate whether systems have reached an equilibrium is to look for non-linearity, asymptotic behaviour or stasis in the eventual long-term dynamics of the system (Hastings, 2004; Isbell, Tilman, et al., 2013). Thus, we performed AIC model selection to determine whether an intercept only, linear, quadratic or saturating function best described convergence within a treatment over the 22-year time series. For our saturating function, we utilized the model $y = \text{Asym} + \left(R_0 - \text{Asym}\right) * \exp(-\exp(\text{lrc}) * \text{year} + \varepsilon)$ due to the ease of interpretation of estimated parameters, where Asym represents the horizontal asymptote of the response variable, R_0 represents the response at year 0 and lrc represents the natural log of the rate constant.

To test if plots receiving different disturbance X nutrient treatments converged or diverged in composition, we calculated the distances between nutrient treatment group centroids (β diversity among treatments) each year for both the disturbed and intact grids. If the distance between group centroids increased over time, this indicated divergence among plots receiving different nutrient treatments (higher β diversity among treatments). As above, we performed AIC model selection to determine what model best described the trend over time. For both within and between nutrient treatments, we compared model parameters across grids (E001 and E002) to see if disturbance altered the rate or asymptotic behaviour of the system. Since convergence or divergence of communities could either be driven by increasing or decreasing similarity among fields, or among replicate plots within the same field, we also report on analyses over time within a field.

Direction and speed of succession

To examine how communities changed through time with disturbance and nutrient addition, we conducted a suite of community trajectory analyses (CTA) (De Cáceres et al., 2019) by projecting data from spatially segregated communities (plots) into a multivariate space, and analysing various geometric properties of their trajectories over time. We defined a multivariate space to study compositional dynamics using the abundance-based Bray–Curtis dissimilarities (d) in community composition among all plots across the time series. We conducted a principal coordinates analysis (PCoA) using the *pcoa* function from package *ape* (Paradis & Schliep, 2019) to summarize the Bray–Curtis dissimilarity matrix in ordination space.

To visualize the directionality of succession, we plotted yearly and decadal trends across disturbance × nutrient treatments. To quantitatively assess directionality of successional pathways, we calculated a directionality index (D) from the function *trajectoryDirectionality* from package *ecotraj*, using the index defined by De Cáceres et al. (2019):

$$D = \frac{\sum \omega_{ijk} \times \frac{(180 - \theta_{ijk})}{180}}{\sum \omega_{ijk}}$$

where $\omega_{ijk} = d(x_i, x_j) + d(x_j, x_k)$ with d representing the Bray-Curtis distance between three community states ordered in time such that $t_i < t_j < t_k$ and θ representing the angle between the three consecutive segments. Values of 0° for θ represent that the three community states are completely aligned in multivariate space, whereas values of 180° indicate that the two vectors are oriented in opposite directions. Directionality indices practically represent the amount of angular change over a given path length with larger values representing straighter, or more directional paths, and smaller values representing more meandering paths.

Lastly, we assessed the speed of succession across disturbance × nutrient treatments, to address whether communities tended towards a stable state with lower temporal turnover, or persisted in a state of long-term transience with high turnover. We calculated trajectory lengths between consecutive annual surveys in the same plots using the *trajectorylengths* function from package *ecotraj* (De Cáceres et al., 2019) and regressing inter-annual trajectory distances calculated from the Bray–Curtis dissimilarity matrix (d) over time. Inter-annual trajectory distances represent the amount of species turnover between years, with larger values indicating more turnover and smaller values indicating similar species composition between years. As above, we performed AIC model selection to which model best described changes in the speed of succession, and if that varied by disturbance X nutrient treatments.

RESULTS

Explained variability and overall trends in community composition

Variation in community composition explained by the disturbance event in 1982 was high (24%) in the first year, but quickly declined to ~1% explained over a period of about 5 years (Figure 1a). Meanwhile, variation explained by annual nutrient application increased steadily over the first decade, and then plateaued at ~40% (range: 37%–44% from years 9–22) (Figure 1b). During the early portion of the time series, variation in community composition was dominated by among-field spatial variation, likely reflective of differences in age since abandonment (Figure S1). During the first 5 years, the three old fields began to converge in composition due to treatment effects, although variation among fields still persisted after 20 years of nutrient addition (range: 10%–19% from years 9–22, Figure 1c). Total aboveground biomass fluctuated throughout the experiment (Figure S3).

Early successional communities that established after the disturbance in 1982 included the C3 grass *Panicum oligosanthes*, the C4 grass *Setaria lutescens* and forbs including *Polygonum convolvulus* (Table 1). In PCoA ordination space, disturbed plots started at lower values of PCoA axis 2 (Figure 2), driven by these early

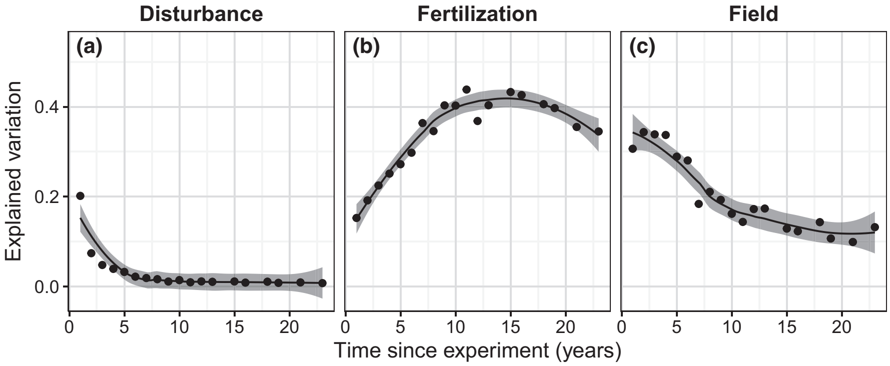

FIGURE 1 Variation in aboveground plant community composition explained by (a) disturbance (disking event in 1982), (b) annual nutrient addition and (c) field identity (A, B, C) from 1982 to 2004. Plotted values are the R^2 of each independent variable from a PERMANOVA model. Lines represent loess fits with 95% confidence intervals.

TABLE 1 Indicator species analysis depicting plants associated with groups based on disturbance (Remnant field D, and three replicate old field grids E001 and E002), nutrients (control and high nutrient plots receiving $27.2\ \text{g} \cdot \text{m}^2 \cdot \text{year}^{-1}$) and timing relative to the start of the experiment (early: 1982–1985, and late: 2000–2004). We allowed for species to be associated with 1 to 4 groups. Species associations were generated using permutation tests for statistical significance. We report only the species with the strongest group associations (test statistic > 0.7), and their associated functional group. Plant functional groups: F = Forb, L = Legume C3 = C3 grass, C4 = C4 grass and S = Sedge.

	Early (1982–1985)				**Late (2000–2004)**			
Remnant	*Poa pratensis*	C3						
	Panicum perlongum	C3						
	Panicum oligosanthes	C3						
	Carex spp.	S			*Carex spp.*	S		
	Ambrosia coronopifolia	F						
	Artemisia ludoviciana	F						
	Rubus sp.	W			*Rubus sp.*	W		
Intact in 1982	Control		High N		Control		High N	
	Schiz. scoparium	C4	*Schiz. scoparium*	C4	*Schiz. scoparium*	C4		
			Agropyron repens	C3	*Poa pratensis*	C3	*Agropyron repens*	C3
			Panicum oligosanthes	C3				
			Poa pratensis	C3				
			Ambrosia coronopifolia	F				
			Artemisia ludoviciana	F				
	Control		High N		Control		High N	
Disturbed in 1982	*Setaria lutescens*	C4	*Setaria lutescens*	C4	*Schiz. scoparium*	C4		
	Panicum oligosanthes	C3	*Agropyron repens*	C3	*Poa pratensis*	C3	*Agropyron repens*	C3
			Panicum oligosanthes	C3				
	Ambrosia coronopifolia	F	*Artemisia ludoviciana*	F	*Lathyrus venosus*	L	*Rubus sp.*	W
	Artemisia ludoviciana	F	*Polygonum convolvulus*	F				
	Polygonum convolvulus	F						

successional species (Figure S4). High nutrient plots in both intact and disturbed grids were pushed towards higher values of PCoA axis 1 characterized by the C3 grass *Agropyron repens* (Figure S4). Meanwhile, control (unfertilized) plots in both intact and disturbed grids were characterized by the C4 grass *Schizachyrium scoparium*. Legumes disappeared from high nutrient plots, but persisted in control plots, regardless of disturbance (Table 1). Even after several decades of agricultural abandonment, old field communities remained distinct from the remnant field D which was characterized by *Carex* spp. and other native grass and forb species (Table 1).

Annual nutrient addition also yielded predictable changes in the dominance of plant functional types (Figure S5). For both the disturbed and intact grids, unfertilized plots had a more even distribution of plant types over the time series, while highly fertilized plots became dominated by C3 grasses (Figure S5). Plot-level species richness (11.8 ± 0.36 species in year 1) declined throughout the experiment at a similar rate in both disturbed and intact grids (Figure S6). The rate and overall amount of decline varied across nutrient treatments, with species richness plateauing at 7.53 ± 0.33 species for the control plots and 3.96 ± 0.21 species for the highly fertilized plots (Figure S6). Field C averaged the highest species richness among the experimental old fields at the beginning and end of the experiment (13.8 ± 0.98 species per plot in year 1 and 10.7 species per plot ±0.76 in year 22 in the E001 grid, Figure S2).

Assessing convergence versus divergence

For both intact and disturbed grids, communities that received the same nutrient supply across fields tended to converge in composition (Figure 3a,b). The average Bray–Curtis distance between each community (plot) to its group centroid (the average of 18 or 9 plots with the same disturbance × nutrient treatment) was best fit with a quadratic function through time (Table S1) where communities rapidly converged during the first decade and either plateaued or began to diverge during second decade (Table S2). Notably, the tendency for plots to diverge in the second decade was driven most strongly by the highest N treatments (17 and $27.2\ \text{g N} \cdot \text{m}^2 \cdot \text{year}^{-1}$). For replicate plots receiving the same nutrient treatment within a field, two of the three old fields (Fields A and B) showed within-field convergence during the first decade regardless of disturbance in 1982, and some variability in the second decade (Figure S7). Meanwhile in Field C, particularly in the intact grid, within-field β diversity among treatments

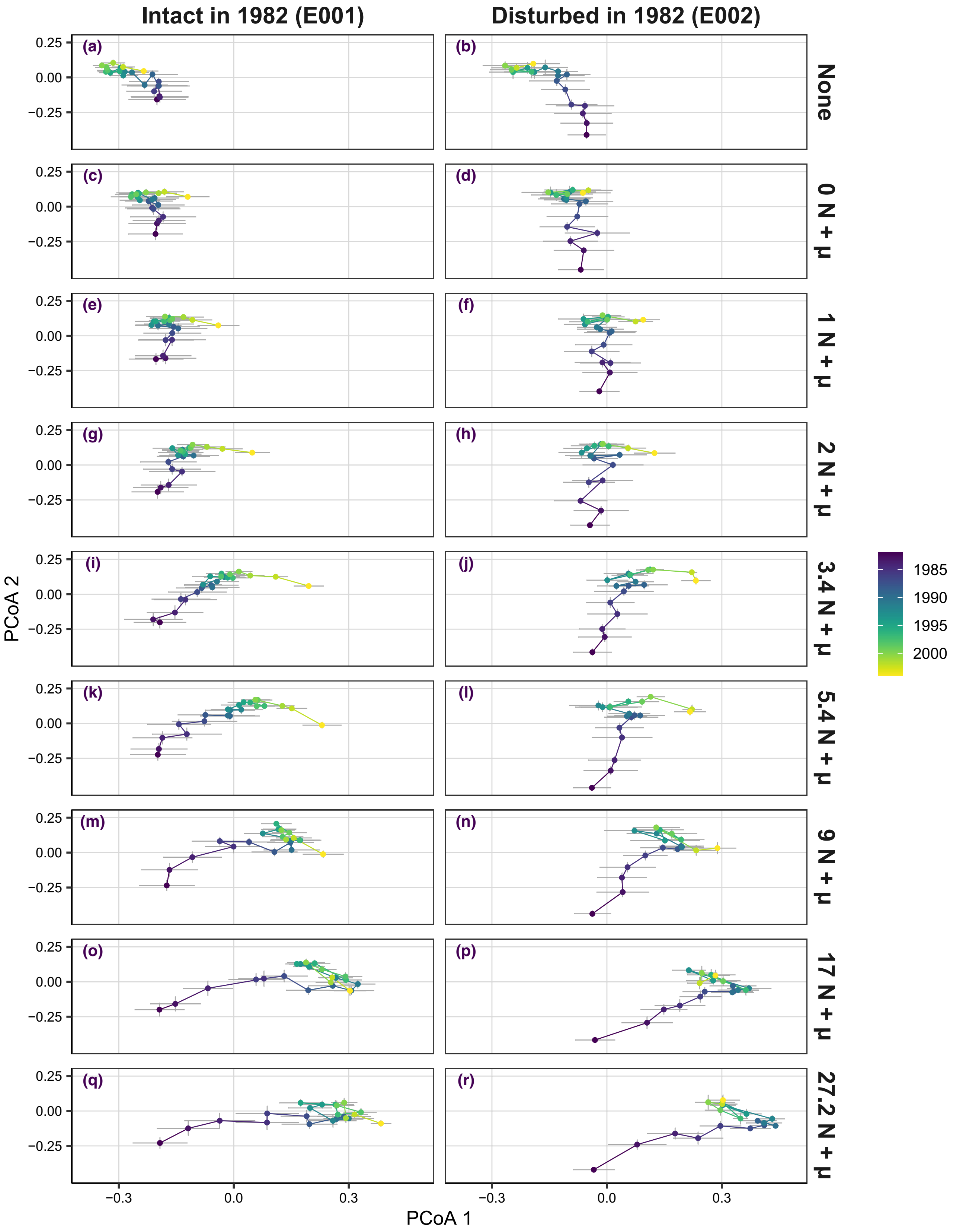

FIGURE 2 Yearly community trajectories in PCoA ordination space. Points represent mean PCoA scores ($n = 18$ for intact and disturbed grid before 1992 and $n = 9$ for disturbed grid after 1992) ±1 SE (in grey bars) from aboveground plant community composition data in intact (left column) and disturbed (right column) communities across annual nutrient addition treatments (rows). Points are connected through time to show yearly trajectories throughout the experiment from 1982 (purple) to 2004 (yellow).

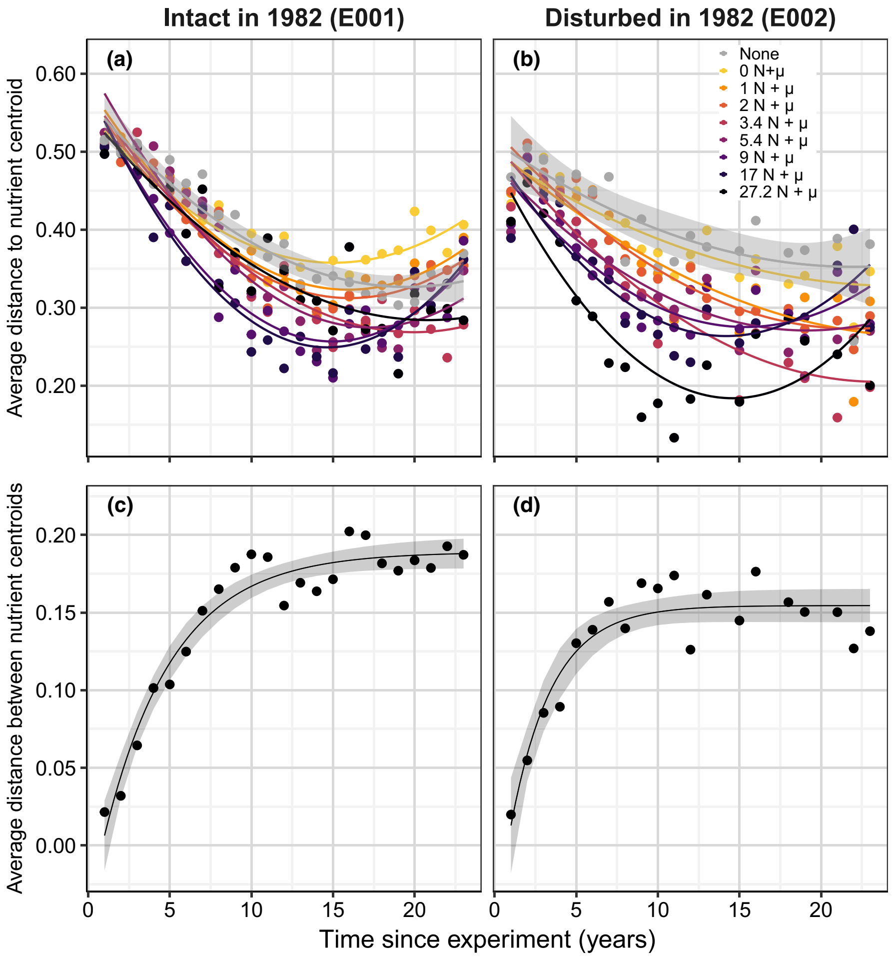

FIGURE 3 (a, b) Average Bray–Curtis distance from each plot to its nutrient treatment group centroid through time in intact (a) and disturbed plots (b). Lines represent quadratic regressions, with 95% confidence intervals shown for the control. AIC values of competing models and parameter estimates for regressions are in Tables S1 and S2. (c, d) Average Bray–Curtis distance between nutrient treatment group centroids through time in intact (c) and disturbed plots (d). Lines represent asymptotic regressions with 95% confidence intervals. AIC values of competing models and parameter estimates for regressions are in Tables S3 and S4.

remained consistent across the time series for all nutrient treatments (Figure S7).

Communities receiving different nutrient treatments within and across fields diverged through time (Figure 3c,d, Figure S8). Bray–Curtis distances between group centroids (across nutrients treatments) were best fit with an increasing saturating function (Figure S3) where the overall level of divergence accumulated rapidly in the first decade of the experiment, and slowed towards an asymptote in the second decade (Figure 3c,d). The distance between nutrient centroids among fields in the intact grid plateaued at 0.174±0.007 while the distance between centroids in the disturbed grid plateaued lower (0.170±0.011, Asym parameter in Table S4). Within all fields, communities receiving different nutrient treatments diverged through time, though the rate of divergence plateaued in Fields B and C but continued to increase in the youngest Field A (Figure S8). Comparing across nutrient treatments in the distance between E001 and E002 group centroids, communities converged during the first decade at a similar rate across nutrient treatments, and either plateaued or diverged in the second decade (Figure S9).

Direction and speed of succession

The directionality of community change, indicating how meandering a community's successional pathway is in multivariate space, showed strong differences with both nutrient addition and disturbance (Figure 4a,b). Directionality was greater in the first decade of the experiment, as communities were in a transient, successional state, and lower in the second decade, as communities reached an equilibrium state (Figure S10). In the intact grids, unfertilized plots had lower directionality (i.e. more meandering) and increasing nutrient supply rate increased directionality, except for the two highest levels of nutrient application (Figure 4a), where this decrease was driven by dynamics during the second decade (Figure S10). Meanwhile in the disturbed grids, directionality was

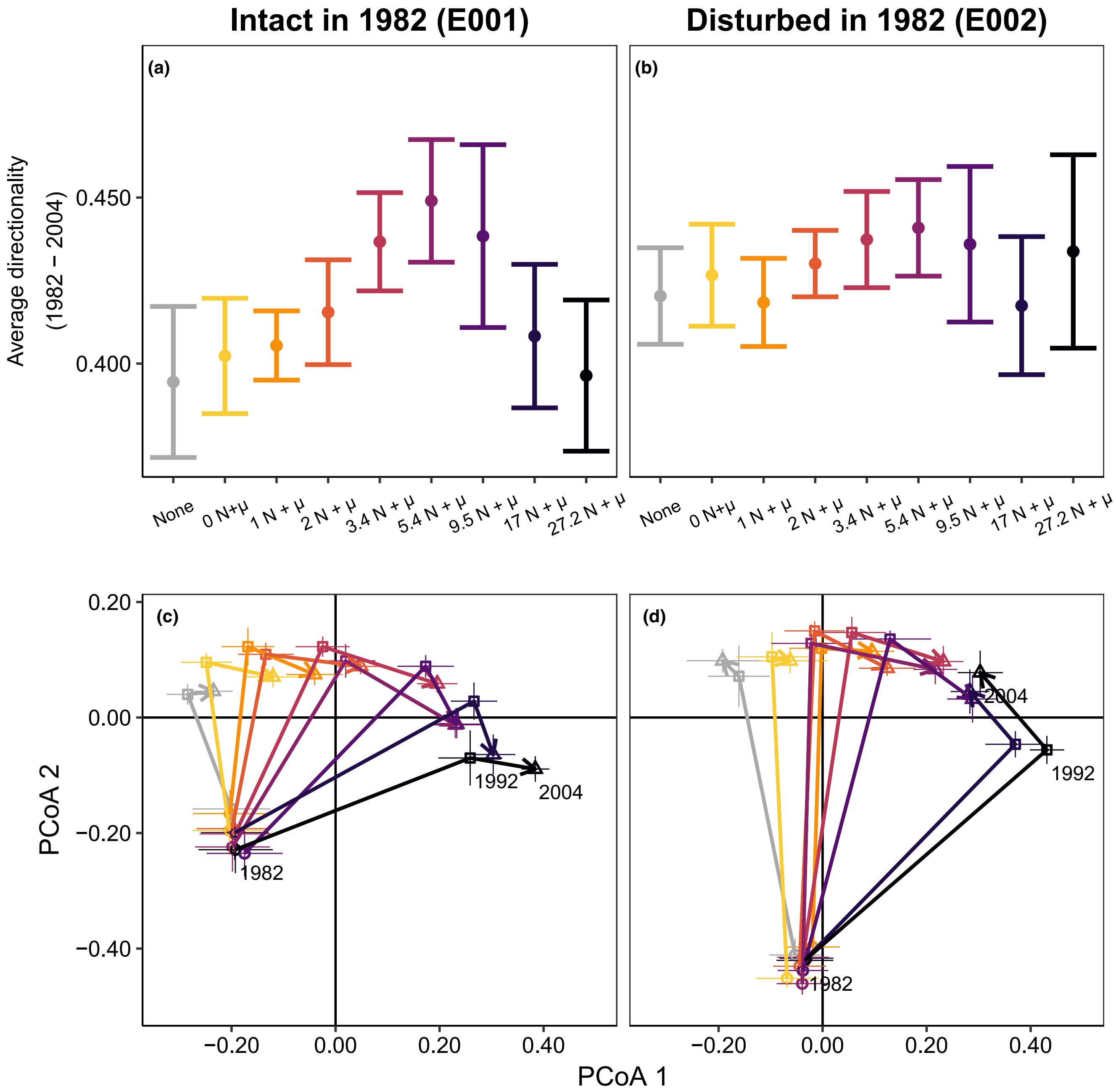

FIGURE 4 Community trajectories including average directionality (a, b) and decadal trajectories (c, d) in PCoA ordination space in intact (a, c) and disturbed (b, d) communities across different levels of nutrient addition. Low directionality in a and b indicate a meandering successional path. Trajectories in c and d are shown for each decade: 1982 (circle) to 1992 (square) and 1992 to 2004 (triangle). Error bars represent 95% confidence intervals (a, b) and ±1 SE (c, d).

greater overall, and did not vary significantly among nutrient treatments (Figure 4b). Interannual community trajectory distance, a measure of temporal turnover, declined by ~33% throughout the experiment for the intact grids, and ~50% for the disturbed grids (Figure 5). This relationship was best described with a decreasing saturation function (Table S5). Community turnover declined at a similar level for most of the nutrient addition treatments in the intact grids, but decreased at a greater rate with increasing nutrients in the disturbed grids (Table S6).

DISCUSSION

Collectively, our results demonstrated that old fields tended towards resource-mediated equilibrium states regardless of whether they were disturbed or intact in 1982 (Figure 4c,d). Most community metrics including species turnover and divergence between centroids displayed asymptotic long-term behaviour, suggesting the emergence of equilibria (Figure 3). Successional trajectories emerged from two processes: convergence within communities with the same nutrient treatments (Figure 3a,b)

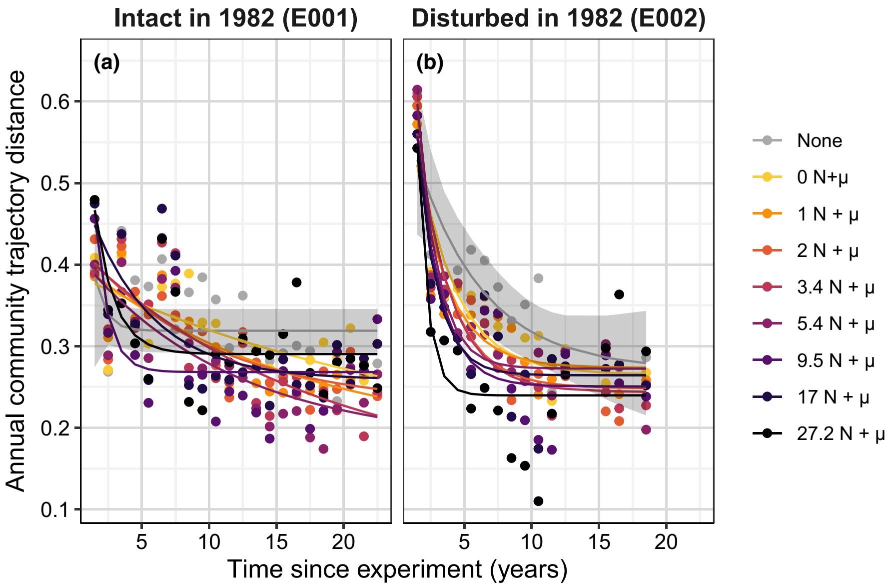

FIGURE 5 Annual community trajectory distance (temporal species turnover) in aboveground plant community composition in intact (a) and disturbed (b) communities across nutrient addition treatments (colours). Points represent the average trajectory distance between consecutive years of plots with the same disturbance × nutrient treatment. Lines represent the decreasing saturating model fit, with 95% confidence intervals shown for the control for clarity.

and divergence between communities with different nutrient treatments (Figure 3c,d). Disturbance altered transience by making the successional pathway more direct (Figure 4b), revealing an important interaction effect between drivers. In particular, species that were favoured by the disturbance event in 1982 were those that came to dominate the highly fertilized plots (Table 1).

Plant communities at Cedar Creek persisted in a distinct phase of transience for approximately 10 years before they appear to settle on dynamic, resource-mediated equilibrium states (Figures 1b and Figure 3). Furthermore, plots that were disturbed in 1982 that were unfertilized or received low levels of nitrogen settled on a higher distance between group centroids compared to their intact old field counterparts, indicating greater levels of spatial β diversity at equilibria (Figure 3a,b). Interannual rates of change in community composition decreased as communities reached equilibrium states (Figure 5); however, communities still experienced relatively high levels of community turnover in the later stages of succession. These results align with a study examining post-agricultural secondary succession in New Jersey where temporal turnover of dominant species decreased over time, but remained relatively high at later successional stages (Li et al., 2016). Both our study and Li et al. (2016) suggest that communities undergoing succession can ultimately settle on a ‘dynamical equilibrium’ or steady-state distribution, rather than a point equilibrium characterized by highly consistent communities. At a steady-state equilibrium, community turnover can still be quite high as communities sample compositions within the steady-state distribution (Naselli-Flores et al., 2003; Shoemaker et al., 2020) (Changes between 1992 and 2004 in Figure 2). Multiple factors, including demographic stochasticity, environmental fluctuations and small-scale spatial heterogeneity (Furey et al., 2022) can yield temporal turnover and variability in community composition at this dynamical equilibrium. Cross-system comparisons could shed light on dynamical equilibria, and how the amount of turnover at an ecosystem's steady-state distribution may depend on species traits (e.g. fast-growing vs. slow-growing systems, seed-banking ability), the size of the species pool, and the inherent amount of environmental variability under which the system has evolved (Chase, 2003; Fernandez-Going et al., 2012).

In our study, replicate experimental old fields varied in some important ways, including time since agricultural abandonment. Though among field differences at Cedar Creek were initially strong, these effects declined as nutrient addition explained more variation in community composition in the first decade of the experiment (Figure 1b,c). These findings generally support Inouye and Tilman's (Inouye & Tilman, 1988) prediction that communities at Cedar Creek would move towards resource-mediated equilibrium states regardless of variation in starting conditions. Nonetheless, field differences at Cedar Creek still represented about ~15% of the variation in community composition after two decades of nutrient addition (Figure 1c), and within-field convergence was variable across fields (Figure S7) suggesting that initial differences did have some consequential and long-term impacts on community composition. In particular, Field C, which had been undergoing secondary succession for almost twice as long as Field B at the beginning of the experiment, had higher species richness and retained higher within-field β diversity among treatments (Figure S2). A recent metaanalysis demonstrated that secondary grasslands, such as the experimental old fields in this study, only represent around 63% of herbaceous plant species richness of old-growth grasslands (Nerlekar & Veldman, 2020). Thus, if this study were conducted in old-growth grasslands with higher species richness, we would expect overall higher levels of β diversity within and among treatments.

The long-term nature of this experiment reveals that nutrient addition and disturbance by tilling yield similar effects on plant composition at Cedar Creek, but they operate on different timescales. Consistent with theory, the annual nutrient addition (press perturbation) created a sustained compositional change, and the emergence of new, nutrient-mediated equilibrium states (Bender et al., 1984), with unfertilized plots dominated by the C4 grass *Schizachyrium scoparium*, a strong competitor for nitrogen, (Wilson & Tilman, 1991) and highly fertilized plots dominated by the rhizomatous C3 grass *Agropyron repens* (Table 1). Since these equilibria took nearly a decade to emerge, it seems unlikely that a pulse nutrient addition occurring once at the beginning of the experiment would have created these distinct, persistent states. In contrast, the disturbance (pulse perturbation) initially had a strong effect on species abundances, but had minimal impacts on long-term composition (Figure 1) (Bender et al., 1984). Importantly, the disturbance treatment restarted the successional process and made pathways more direct (Figure 4), favouring species that eventually came to dominate the fertilized plots (Table 1). Soil disturbances, such as tilling, typically create environments with high levels of light and low levels of competition. Tilling also aerates the soil which can cause a short-term release of nitrogen (Hassink, 1992; Kristensen et al., 2003). A variety of models suggest that recently disturbed patches become colonized by fast-growing species that are poor resource competitors (Bolker & Pacala, 1999; Pacala & Rees, 1998) consistent with the competition-colonization trade-off, a stabilizing force for coexistence (Hastings, 1980; Levins & Culver, 1971). This relationship is apparent at our study site, where disturbance initially favoured early successional species that tend to have high fecundity and dispersal ability (Sullivan et al., 2018) and low nitrogen-use efficiency (Tilman, 1994). Had disturbance occurred annually instead of once at the beginning of the experiment, this transient period would likely persist for longer, characterized by these fast-growing species (Bolker & Pacala, 1999; Pacala & Rees, 1998). The coupling of species that prefer disturbance and high-resource requirements may not occur in other systems or for other types of disturbance. For example, fires tend to reduce limiting nutrient availability and severe disturbances that initiate primary succession (e.g. glaciation or volcanoes) can create very harsh low nutrient environments. In these cases, the early colonizers must be nutrient efficient (e.g. nitrogen-fixers), which are ultimately at a disadvantage in higher nutrient environments (Tognetti et al., 2021).

CONCLUSION

Our study examined competing theories of community assembly (HilleRisLambers et al., 2012; Kraft et al., 2015), stability (Connell & Slatyer, 1977; Hallett et al., 2018) and coexistence (Tilman, 1985) while informing potential future avenues of theoretical development using community metrics that capture the speed and direction of community change over time (De Cáceres et al., 2019). Taken together, our results imply that grassland communities at Cedar Creek tended towards resource-mediated equilibrium states regardless of initial conditions, but that disturbance made successional pathways more direct. In particular, disturbance moved successional trajectories towards changes eventually induced by nutrient addition. Importantly, our results also demonstrated that the rate of community turnover can remain high as communities approach and reach equilibrium states (Figure 5). As such, we advocate that future work on succession and community assembly incorporate fluctuation dependent coexistence and stochastic theory, as communities at their dynamical equilibrium can be highly variable (Aoyama et al., 2022; Hallett et al., 2019; Shoemaker et al., 2020).

AUTHOR CONTRIBUTION

Lauren L. Sullivan, Lauren G. Shoemaker and Melissa H. DeSiervo conceived the idea for the article. Melissa H. DeSiervo analysed the data and wrote the first draft of the article. Lauren L. Sullivan, Larissa M. Kahan, Eric W. Seabloom and Lauren G. Shoemaker contributed on the figures and analyses, discussion and article revisions.

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DATA AVAILABILITY STATEMENT

Data and code are available on GitHub: https://github.com/melissadesiervo1031/CedarCreekconvergence.

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