

# 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 favored by the disturbance were those that eventually came to dominate the highly fertilized plots. Furthermore, disturbance made successional pathways more direct under low nutrients, 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 beta-diversity change through transient and equilibrium states.

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

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# 1 **Abstract**

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

## 16 Introduction

17 Temporal change in ecological communities has long fascinated ecologists, prompting a  
18 rich study of succession that underpins many theories in community ecology (Clements,  
19 1916; Gleason, 1926; Pickett *et al.*, 2009; Chang *et al.*, 2019). In the modern era of rapid  
20 environmental change, ecological disturbances and temporal dynamics are now interacting  
21 with multiple global change drivers known to influence community composition and structure  
22 (Chang *et al.*, 2019). Consequently, there is a renewed interest in updating our understanding  
23 of succession through data-theory integration using contemporary approaches that capture  
24 the complex determinants of community composition change (Avolio *et al.*, 2021). A recent  
25 metaanalysis of global change experiments in herbaceous plant communities determined that  
26 the effects of multiple global change drivers on communities were typically synergistic, but  
27 lagged, and often only detectable over long ( $\geq 10$  years) timescales (Komatsu *et al.*, 2019).  
28 Building on foundational theory of ecological succession and community assembly is essential  
29 for understanding community responses to anthropogenic drivers of change, and to improve  
30 conservation and restoration outcomes in a rapidly changing world (Chang *et al.*, 2019;  
31 Komatsu *et al.*, 2019).

32 Early models in successional theory predicted that communities change directionally  
33 over time towards a climax system (Clements, 1916; Lepš & Rejmánek, 1991; Pickett *et al.*,  
34 2009). Inherent in this historical paradigm of succession is convergence: a process where  
35 spatially segregated communities equilibrate to the same species composition and structure  
36 regardless of underlying spatiotemporal variability in starting conditions. The final stable  
37 state community, which persists in perpetuity until a disturbance restarts the successional  
38 process, consists of a suite of coexisting species with stable population dynamics (Law, 1999).  
39 Resource-based competition models of community structure (e.g.,  $R^*$  theory) predict that  
40 nutrient supply rate is the primary determinant of equilibrium plant community assemblages,

41 assuming all species can reach all locations (Tilman & Wedin, 1991; Wilson & Tilman, 1991,  
42 1993; Tilman, 1985) and that spatially segregated communities with the same nutrient supply  
43 will converge on similar species composition, regardless of disturbance or variable starting  
44 conditions(Inouye & Tilman, 1988). A change in nutrient supply, however, is predicted to  
45 shift the equilibrium community towards a new, possibly irreversible stable state (Suding  
46 *et al.*, 2004). For example in the grassland system we focus on here, Isbell *et al.* (2013a)  
47 found that plant communities persisted in a low-diversity state more than two decades after  
48 the cessation of nutrients, suggesting that fertilization caused a regime shift.

49 Directly contradicting a predictable, resource-based competition paradigm of succession,  
50 more recent theory has emphasized how stochastic and heterogeneous factors including small  
51 scale abiotic variation, probabilistic dispersal, colonization, and local extinction can lead to  
52 divergent communities that exhibit alternative stable states (Fukami & Nakajima, 2011;  
53 Fukami, 2015; Shoemaker *et al.*, 2020; Miller *et al.*, 2021). Priority effects including niche  
54 preemption and modification from early arriving species can result in multiple, alternative  
55 steady state pathways across locations that had different species arrival order, even under  
56 the same environmental conditions (Fukami, 2015). For example, Chase’s (2003) mesocosm  
57 study demonstrated that successional trajectories in aquatic mesocosms with intermediate  
58 productivity exhibited alternative stable states depending on the initial density of a sin-  
59 gle organism (snails). Evidence for alternative steady state pathways also occurs in plant  
60 systems. For example, one empirical study examining patterns of plant succession after  
61 the eruption of Mt. St. Helens found evidence for multiple successional pathways within  
62 and among sites, which the authors attribute to the interaction of disturbance, spatial con-  
63 tingencies, and other chance factors (Chang *et al.*, 2019). Theoretical modelling suggests  
64 that divergence between communities is more likely to occur with a large species pool, low  
65 connectivity, high productivity, and infrequent disturbance (Chase, 2003). In parallel, di-  
66 vergence can also depend on small-scale local heterogeneity (spatial contingencies) (Young

67 *et al.*, 2017; Kardol *et al.*, 2007) and the environmental drivers experienced at a single point  
68 in time, especially early in succession (Werner *et al.*, 2020).

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

86     Characterizing successional trajectories in practice necessitates high spatial and tempo-  
87 ral replication that can capture the long-term behavior of the system (Hastings, 2004, 2010;  
88 Inouye & Tilman, 1988). Thus, there are few experimental studies in plant communities  
89 with time series sufficiently long to capture asymptotic trends in community composition  
90 and to distinguish between competing theories of successional dynamics (Hastings, 2004,  
91 2010). To address this knowledge gap, we analyzed a long-term (22 year) experiment from  
92 the Cedar Creek Ecosystem Reserve in Minnesota, USA to examine community succession

93 in three old fields experiencing two anthropogenic drivers of change: soil-tilling disturbance  
94 and nutrient addition. This is an ideal system to examine succession due to a long history  
95 of study at Cedar Creek (Tilman, 1987; Wilson & Tilman, 1991, 1993; Isbell *et al.*, 2013a),  
96 including a rich natural history knowledge base of the common species in this system (Sulli-  
97 van *et al.*, 2018; Catford *et al.*, 2019). We focus on the joint effects of both drivers, as both  
98 community response to nutrient supply (Tilman, 1987; Wilson & Tilman, 1991, 1993; Isbell  
99 *et al.*, 2013a) and recovery from agricultural disturbance (Holt *et al.*, 1995; Debussche *et al.*,  
100 1996; Li *et al.*, 2016; Pickett *et al.*, 2009; Isbell *et al.*, 2019; Nerlekar & Veldman, 2020) have  
101 been well-studied individually, but their joint effects are less understood (Seabloom *et al.*,  
102 2020). If communities at Cedar Creek tend towards alternative stable states or prolonged  
103 transience, disturbance could alter the predictions from adding nutrients alone. An earlier  
104 short-term analysis of successional change from Cedar Creek found that species composi-  
105 tion changed rapidly in response to nutrient addition, but that four years was insufficient  
106 to determine community convergence to resource-controlled equilibria versus divergence or  
107 long-term transience (Inouye & Tilman, 1988). A more recent analysis from Cedar Creek  
108 suggests an interactive effect between nutrients and disturbance on species diversity and total  
109 biomass that emerges after a decade of recovery (Seabloom *et al.*, 2020); however this study  
110 did not evaluate the joint effects of nutrients and disturbance on community composition  
111 nor successional trajectories.

112 Here, we revisited Inouye and Tilman's (1988) initial investigation of succession, extend-  
113 ing from their focus on convergence versus divergence to additionally ask: 1) Do communities  
114 tend towards equilibrium states, remain in long-term transience, or reach alternative stable  
115 states? 2) Do soil resources determine long-term composition? and 3) Are successional  
116 trajectories altered by disturbance? To address whether communities settled into a steady  
117 state, or persisted in long-term transience, we examined the rate of community compositional  
118 change between years, and the directionality of those changes. If communities progressed

119 along a successional pathway towards a stable equilibrium (single or multiple equilibria),  
120 then we expected community turnover to decline, and community trajectories to display  
121 directionality in multivariate space as they move towards equilibria. To address whether  
122 nutrient addition led to the development of resource-controlled equilibria, or if disturbance  
123 or variable starting conditions yielded alternative stable states, we looked for evidence of  
124 convergence or divergence in composition between spatially segregated communities within  
125 and across experimental treatments and fields.

## 126 **Materials and methods**

### 127 **Study site and data collection**

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

135 The experimental design is described briefly here, with additional details in Tilman (1987)  
136 and Seabloom *et al.* (2020). In 1982, identical disturbance X nutrient addition experiments  
137 were established in three abandoned agricultural fields within 5 km of one another that were  
138 last tilled and farmed in 1968 (Field A), 1957 (Field B), and 1934 (Field C). Field A and  
139 Field B were last planted with soybeans, while Field C was last planted with corn. Previous  
140 research at Cedar Creek suggests that soil N increases with time since agricultural aban-  
141 donment (Tilman, 1987; Inouye & Tilman, 1988); consistent with that pattern, Field C had  
142 the highest soil N concentration (638 mg / kg) in 1982 before experimentation. Inconsistent

143 with this pattern, Field B had the lowest soil N concentration (377 mg / kg) while Field  
144 A, the youngest field, was intermediate (582 mg / kg). Prior to the experiment, Field A  
145 was dominated by the C3 grass *Agropyron repens*, while both Field B and Field C were  
146 dominated by the C4 grass *Schizachyrium scoparium* and Field C also had some scattered  
147 *Quercus* seedlings, but no mature trees.

148 Within each of the three Fields, two grids (35 X 55 m) were established in 1982 for  
149 nutrient application, one in an area that was thoroughly disked in the spring of 1982 (E002),  
150 and another in an adjacent area that remained intact with old field vegetation (E001).  
151 The disking treatment pulverized the existing vegetation, leaving bare soil which was then  
152 raked to remove clumps of vegetation. Each grid consisted of 54, 4 X 4 m vegetation plots,  
153 receiving one of nine nutrient treatments (applied annually in May or June) in a randomized  
154 block design, with 6 replicate plots per field. Nitrogen was added as  $\text{NH}_4\text{NO}_3$  and the  
155 micronutrients ( $\mu$ ) consisted of of P, K, Ca, Mg, S and citrate-chelated trace metals ( $\text{P}_2\text{O}_5$   
156 at  $20 \text{ g} \cdot \text{m}^2 \cdot \text{year}^{-1}$ ,  $\text{K}_2\text{O}$  at  $20 \text{ g} \cdot \text{m}^2 \cdot \text{year}^{-1}$ ,  $\text{CaCO}_3$  at  $40 \text{ g} \cdot \text{m}^2 \cdot \text{year}^{-1}$ ,  $\text{MgSO}_4$  at  $30 \text{ g} \cdot \text{m}^2$   
157  $\cdot \text{year}^{-1}$ ,  $\text{CuSO}_4$  at  $18 \text{ } \mu\text{g} \cdot \text{m}^2 \cdot \text{year}^{-1}$ ,  $\text{ZnSO}_4$  at  $37.7 \text{ } \mu\text{g} \cdot \text{m}^2 \cdot \text{year}^{-1}$ ,  $\text{CoCO}_2$  at  $15.3 \text{ } \mu\text{g} \cdot \text{m}^2$   
158  $\cdot \text{year}^{-1}$ ,  $\text{MnCl}_2$  at  $322.0 \text{ } \mu\text{g} \cdot \text{m}^2 \cdot \text{year}^{-1}$ , and  $\text{NaMoO}_4$  at  $15.1 \text{ } \mu\text{g} \cdot \text{m}^2 \cdot \text{year}^{-1}$ ). Importantly,  
159 the soil disking (hereafter referred to as the disturbance treatment) occurred once at the  
160 beginning of the experiment, while the nutrient additions were applied annually throughout  
161 the experiment.

162 Though our emphasis is on the successional trajectories of the three old fields with the  
163 disturbance X nutrient treatments (Fields A, B, and C), a nearby remnant grassland within  
164 a native oak savannah (Field D) that had never been clear-cut or plowed was also surveyed  
165 annually and provides a comparison for our study. In 1982, Field D had a soil N concentration  
166 of 593 mg / kg, (comparable with both Field A and Field C) and was dominated by *Carex*  
167 spp. After the first vegetation survey of plots in summer 1982, the vegetation composition  
168 of the intact grids of Field C and B most closely resembled the remnant Field D (Figure S1).

169 In contrast, the composition of the intact grid of Field A was distinct from Field D, and all  
170 recently disturbed grids were distinct from Field D (Figure S1). After the first vegetation  
171 survey of plots in summer 1982, Field D had the highest species richness at 15.7 species per  
172 plot, followed by the unfertilized control plots in the intact grid of Field C, at 13.8 species  
173 per plot (Figure S2).

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

## 188 **Statistical Analyses**

### 189 **Explained variability and overall trends in community composition**

190 To assess how the disturbance event in 1982, yearly nutrient application, and historical  
191 contingencies of each field explained community composition throughout the experiment,  
192 we used a Permutational ANOVA (PERMANOVA) using the *adonis* function from package

193 *vegan* (Oksanen *et al.*, 2008) in R version 4.1.2 (R Core Team, 2020) with the Bray-Curtis  
194 dissimilarity matrix generated from species' biomass data from all plots for each year from  
195 1982 to 2004. The Bray-Curtis matrix of a given year was the dependent variable, with three  
196 additive independent variables: disturbance (categorical), nutrient treatment (continuous  
197 from 0 to 27.2 g · m<sup>2</sup> · year<sup>-1</sup>), and field (categorical). We included field as a fixed effect,  
198 as we were interested in how differences among fields from variable legacies of agricultural  
199 abandonment may explain differences in composition through time. We examined yearly  
200 trends in the explained variation (partial R<sup>2</sup>) for each independent variable over the 22 years  
201 of the experiment in the PERMANOVA model, evaluating which variables explained the  
202 most variation in community composition, and the longevity of those effects.

203 To provide context for our multivariate results, we report trends in biomass, species  
204 richness, and the relative proportion of plant functional groups across disturbance X nu-  
205 trient treatments. To determine which plant species were driving variation in composition  
206 we performed an indicator species analysis using the *multipatt* function from package *indic-*  
207 *species* (De Caceres & Legendre, 2009) in R. Indicator species analyses assess the association  
208 between species patterns and combinations of groups of sites, and perform permutation tests  
209 for statistical significance of the best matching associations (De Caceres & Legendre, 2009).  
210 For the analysis we grouped sites according to disturbance treatment (remnant field D, and  
211 grids E001 and E002), nutrient treatment (control and 27.2 g N · m<sup>2</sup> · year<sup>-1</sup> plots only) and  
212 timing relative to the start of the experiment (early: 1982 - 1985, and late: 2000 - 2004). We  
213 constrained the analysis to include species associated with one to four of the aforementioned  
214 groups, and we report species with the highest group associations.

### 215 **Assessing convergence vs. divergence**

216 To test if plots receiving the same disturbance X nutrient treatment converged or di-  
217 verged in community composition over time ( $\beta$  diversity), we calculated the average Bray-

218 Curtis distance of replicate communities within treatments to their group centroids using  
219 the *betadisper* function from the R package *vegan* (Oksanen *et al.*, 2008). If the distance  
220 between plots to their group centroids declined over time, this indicated convergence (lower  
221  $\beta$  diversity among plots within a treatment). We evaluated trends of the average distance  
222 to the centroid over the 22-year time series for each disturbance X nutrient treatment. One  
223 way to evaluate whether systems have reached an equilibrium is to look for nonlinearity,  
224 asymptotic behavior, or stasis in the eventual long-term dynamics of the system (Hastings,  
225 2004; Isbell *et al.*, 2013b). Thus, we performed AIC model selection to determine whether  
226 an intercept only, linear, quadratic, or saturating function best described convergence within  
227 a treatment over the 22-year time series. For our saturating function, we utilized the model  
228  $y = Asym + (R_0 - Asym) * \exp(-\exp(lrc) * year + \epsilon)$  due to the ease of interpretation  
229 of estimated parameters, where *Asym* represents the horizontal asymptote of the response  
230 variable,  $R_0$  represents the response at year 0 and *lrc* represents the natural log of the rate  
231 constant.

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

243 **Direction and speed of succession**

244 To examine how communities changed through time with disturbance and nutrient ad-  
245 dition, we conducted a suite of community trajectory analyses (CTA) (De Cáceres *et al.*,  
246 2019) by projecting data from spatially segregated communities (plots) into a multivari-  
247 ate space, and analyzing various geometric properties of their trajectories over time. We  
248 defined a multivariate space to study compositional dynamics using the abundance-based  
249 Bray-Curtis dissimilarities ( $d$ ) in community composition among all plots across the time  
250 series. We conducted a principal coordinates analysis (PCoA) using the *pcoa* function from  
251 package *ape* (Paradis & Schliep, 2019) to summarize the Bray-Curtis dissimilarity matrix in  
252 ordination space.

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

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

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

260 Lastly, we assessed the speed of succession across disturbance X nutrient regimes, to  
261 address whether communities tended towards a stable state with lower temporal turnover,

262 or persisted in a state of long-term transience with high turnover. We calculated trajectory  
263 lengths between consecutive annual surveys in the same plots using the *trajectorylengths*  
264 function from package *ecotraj* (De Cáceres *et al.*, 2019) and regressing inter-annual trajectory  
265 distances calculated from the Bray-Curtis dissimilarity matrix ( $d$ ) over time. Inter-annual  
266 trajectory distances represent the amount of species turnover between years, with larger  
267 values indicating more turnover and smaller values indicating similar species composition  
268 between years. As above, we performed AIC model selection to which model best described  
269 changes in the speed of succession, and if that varied by disturbance X nutrient treatments.

## 270 Results

### 271 Explained variability and overall trends in community composition

272 Variation in community composition explained by the disturbance event in 1982 was high  
273 (24%) in the first year, but quickly declined to  $\sim 1\%$  explained over a period of about five  
274 years (Figure 1a). Meanwhile, variation explained by annual nutrient application increased  
275 steadily over the first decade, and then plateaued at  $\sim 40\%$  (range 37-44% from years 9  
276 to 22) (Figure 1b). During the early portion of the time series, variation in community  
277 composition was dominated by among-field spatial variation, likely reflective of differences  
278 in age since abandonment (Figure S1). During the first 5 years, the three old fields began  
279 to converge in composition due to treatment effects, although variation among fields still  
280 persisted after 20 years of nutrient addition (range 10-19% from years 9 to 22 , Figure 1c).  
281 Total aboveground biomass fluctuated throughout the experiment (Figure S3).

282 Early successional communities that established after the disturbance in 1982 included  
283 the C3 grass *Panicum oligosanthos*, the C4 grass *Setaria lutescens*, and forbs including  
284 *Polygonum convolvulus* (Table 1). In PCoA ordination space, disturbed plots started at  
285 lower values of PCoA axis 2 (Figure 2), driven by these early successional species (Figure S4).

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

293 Annual nutrient addition also yielded predictable changes in the dominance of plant  
294 functional types (Figure S5). For both the disturbed and intact grids, unfertilized plots  
295 had a more even distribution of plant types over the time series, while highly fertilized plots  
296 became dominated by C3 grasses (Figure S5). Plot-level species richness ( $11.8 \pm 0.36$  species  
297 in year 1) declined throughout the experiment at a similar rate in both disturbed and intact  
298 grids (Figure S6). The rate and overall amount of decline varied across nutrient treatments,  
299 with species richness plateauing at  $7.53 \pm 0.33$  species for the control plots and  $3.96 \pm$   
300  $0.21$  species for the highly fertilized plots (Figure S6). Field C averaged the highest species  
301 richness among the experimental old fields at the beginning and end of the experiment ( $13.8$   
302  $\pm 0.98$  species per plot in year 1 and  $10.7$  species per plot  $\pm 0.76$  in year 22 in the E001  
303 grid, Figure S2).

#### 304 **Assessing convergence vs. divergence**

305 For both intact and disturbed grids, communities that received the same nutrient supply  
306 across fields tended to converge in composition (Figure 3 a, b). The average Bray-Curtis  
307 distance between each community (plot) to its group centroid (the average of 18 or 9 plots  
308 with the same disturbance X nutrient regime) was best fit with a quadratic function through  
309 time (Table S1) where communities rapidly converged during the first decade and either  
310 plateaued or began to diverge during second decade (Table S2). Notably, the tendency for

311 plots to diverge in the second decade was driven most strongly by the highest N treatments  
312 (17 and 27.2 g N · m<sup>2</sup> · year<sup>-1</sup>). For replicate plots receiving the same nutrient treatment  
313 within a field, two of the three old fields (Fields A and B) showed within-field convergence  
314 during the first decade regardless of disturbance in 1982, and some variability in the sec-  
315 ond decade (Figure S7). Meanwhile in Field C, particularly in the intact grid, within-field  
316  $\beta$  diversity among treatments remained consistent across the time series for all nutrient  
317 treatments (Figure S7).

318 Communities receiving different nutrient treatments within and across fields diverged  
319 through time (Figure 3 c, d, Figure S8). Bray-Curtis distances between group centroids  
320 (across nutrients treatments) were best fit with an increasing saturating function (Table S3)  
321 where the overall level of divergence accumulated rapidly in the first decade of the experi-  
322 ment, and slowed towards an asymptote in the second decade (Figure 3 c, d). The distance  
323 between centroids among fields in the intact grid plateaued at  $0.174 \pm 0.007$  while the  
324 distance between centroids in the disturbed grid plateaued lower ( $0.170 \pm 0.011$ , *Asym* pa-  
325 rameter in Table S4). Within all fields, communities receiving different nutrient treatments  
326 diverged through time, though the rate of divergence plateaued in Fields B and C but contin-  
327 ued to increase in the youngest Field A (Figure S8). Comparing across nutrient treatments  
328 in the distance between E001 and E002 group centroids, communities converged during the  
329 first decade at a similar rate across nutrient treatments, and either plateaued or diverged in  
330 the second decade (Figure S9).

### 331 **Direction and speed of succession**

332 The directionality of community change, indicating how meandering a community's suc-  
333 cessional pathway is in multivariate space, showed strong differences with both nutrient  
334 addition and disturbance (Figure 4 a and b). Directionality was greater in the first decade of  
335 the experiment, as communities were in a transient, successional state, and lower in the sec-

336 ond decade, as communities reached an equilibrium state (Figure S10). In the intact grids,  
337 unfertilized plots had lower directionality (i.e. more meandering) and increasing nutrient  
338 supply rate increased directionality, except for the two highest levels of nutrient applica-  
339 tion (Figure 4 a), where this decrease was driven by dynamics during the second decade  
340 (Figure S10). Meanwhile in the disturbed grids, directionality was greater overall, and did  
341 not vary significantly among nutrient treatments (Figure 4 b). Interannual community tra-  
342 jectory distance, a measure of temporal turnover, declined by around 33% throughout the  
343 experiment for the intact grids, and around 50% for the disturbed grids (Figure 5). This  
344 relationship was best described with a decreasing saturation function (Table S5). Commu-  
345 nity turnover declined at a similar level for most of the nutrient addition treatments in the  
346 intact grids, but decreased at a greater rate with increasing nutrients in the disturbed grids  
347 (Table S6).

## 348 Discussion

349 Collectively, our results demonstrated that old fields tended towards resource-mediated  
350 equilibrium states regardless of whether they were disturbed or intact in 1982 (Figure 4 c,  
351 d). Most community metrics including species turnover and divergence between centroids  
352 displayed asymptotic long-term behavior, suggesting the emergence of equilibria (Figure 3).  
353 Successional trajectories emerged from two processes: convergence within communities with  
354 the same nutrient treatments (Figure 3 a, b) and divergence between communities with  
355 different nutrient treatments (Figure 3 c, d). Disturbance altered transience by making the  
356 successional pathway more direct (Figure 4 b), revealing an important interaction effect  
357 between drivers. In particular, species that were favored by the disturbance event in 1982  
358 were those that came to dominate the highly fertilized plots (Table 1).

359 Plant communities at Cedar Creek persisted in a distinct phase of transience for approx-

360 imately 10 years before they appear to settle on dynamic, resource-mediated equilibrium  
361 states (Figure 1 b, Figure 3). Furthermore, plots that were disturbed in 1982 that were  
362 unfertilized or received low levels of nitrogen settled on a higher distance between group  
363 centroids compared to their intact old field counterparts, indicating greater levels of spa-  
364 tial beta diversity at equilibria (Figure 3 a , b). Interannual rates of change in community  
365 composition decreased as communities reached equilibrium states (Figure 5); however com-  
366 munities still experienced relatively high levels of community turnover in the later stages  
367 of succession. These results align with a study examining post-agricultural secondary suc-  
368 cession in New Jersey where temporal turnover of dominant species decreased over time,  
369 but remained relatively high at later successional stages (Li *et al.*, 2016). Both our study  
370 and Li *et al.* (2016) suggest that communities undergoing succession can ultimately settle  
371 on a “dynamical equilibrium” or steady state distribution, rather than a point equilibrium  
372 characterized by highly consistent communities. At a steady state equilibrium, commu-  
373 nity turnover can still be quite high as communities sample compositions within the steady  
374 state distribution (Naselli-Flores *et al.*, 2003; Shoemaker *et al.*, 2020) (Changes between  
375 1992 and 2004 in Figure 2). Multiple factors, including demographic stochasticity, envi-  
376 ronmental fluctuations, and small-scale spatial heterogeneity (Furey *et al.*, 2022) can yield  
377 temporal turnover and variability in community composition at this dynamical equilibrium.  
378 Cross-system comparisons could shed light on dynamical equilibria, and how the amount  
379 of turnover at an ecosystem’s steady state distribution may depend on species traits (e.g.  
380 fast-growing versus slow-growing systems, seedbanking ability), the size of the species pool,  
381 and the inherent amount of environmental variability under which the system has evolved  
382 (Chase, 2003; Fernandez-Going *et al.*, 2012).

383 In our study, replicate experimental old fields varied in some important ways, including  
384 time since agricultural abandonment. Though among field differences at Cedar Creek were  
385 initially strong, these effects declined as nutrient addition explained more variation in com-

386 munity composition in the first decade of the experiment (Figure 1 b, c). These findings  
387 generally support Inouye and Tilman’s (1988) prediction that communities at Cedar Creek  
388 would move towards resource-mediated equilibrium states regardless of variation in starting  
389 conditions. Nonetheless, field differences at Cedar Creek still represented about  $> 15\%$  of  
390 the variation in community composition after two decades of nutrient addition (Figure 1  
391 c), and within-field convergence was variable across fields (Figure S7) suggesting that initial  
392 differences did have some consequential and long-term impacts on community composition.  
393 In particular, Field C, which had been undergoing secondary succession for almost twice  
394 as long as Field B at the beginning of the experiment, had higher species richness and re-  
395 tained higher within-field  $\beta$  diversity among treatments (Figure S7). A recent metaanalysis  
396 demonstrated that secondary grasslands, such as the experimental old fields in this study,  
397 only represent around 63% of herbaceous plant species richness of old-growth grasslands  
398 (Nerlekar & Veldman, 2020). Thus, if this study were conducted in old-growth grasslands  
399 with higher species richness, we would expect overall higher levels of  $\beta$  diversity within and  
400 among treatments.

401 The long-term nature of this experiment reveals that nutrient addition and disturbance  
402 by tilling yield similar effects on plant composition at Cedar Creek, but they operate on  
403 different time scales. Consistent with theory, the annual nutrient addition (press perturba-  
404 tion) created a sustained compositional change, and the emergence of new, nutrient-mediated  
405 equilibrium states (Bender *et al.*, 1984), with unfertilized plots dominated by the C4 grass  
406 *Schizachyrium scoparium*, a strong competitor for nitrogen, (Wilson & Tilman, 1991), and  
407 highly fertilized plots dominated by the rhizomatous C3 grass *Agropyron repens* (Table 1).  
408 Since these equilibria took nearly a decade to emerge, it seems unlikely that a pulse nutri-  
409 ent addition occurring once at the beginning of the experiment would have created these  
410 distinct, persistent states. In contrast, the disturbance (pulse perturbation) initially had  
411 a strong effect on species abundances, but had minimal impacts on long-term composition

412 (Figure 1) (Bender *et al.*, 1984). Importantly, the disturbance treatment restarted the suc-  
413 cessional process and made pathways more direct (Figure 4), favoring species that eventually  
414 came to dominate the fertilized plots (Table 1). Soil disturbances, such as tilling, typically  
415 create environments with high levels of light and low levels of competition. Tilling also  
416 aerates the soil which can cause a short-term release of nitrogen (Hassink, 1992; Kristensen  
417 *et al.*, 2003). A variety of models suggest that recently disturbed patches become colonized  
418 by fast-growing species that are poor resource competitors (Bolker & Pacala, 1999; Pacala  
419 & Rees, 1998) consistent with the competition-colonization tradeoff, a stabilizing force for  
420 coexistence (Hastings, 1980; Levins & Culver, 1971). This relationship is apparent at our  
421 study site, where disturbance initially favored early successional species that tend to have  
422 high fecundity and dispersal ability (Sullivan *et al.*, 2018) and low nitrogen-use efficiency  
423 (Tilman, 1994). Had disturbance occurred annually instead of once at the beginning of  
424 the experiment, this transient period would likely persist for longer, characterized by these  
425 fast-growing species (Bolker & Pacala, 1999; Pacala & Rees, 1998). The coupling of species  
426 that prefer disturbance and high-resource requirements may not occur in other systems or  
427 for other types of disturbance. For example, fires tend to reduce limiting nutrient availabil-  
428 ity and severe disturbances that initiate primary succession (e.g., glaciation or volcanoes)  
429 can create very harsh low nutrient environments. In these cases, the early colonizers must  
430 be nutrient efficient (e.g., nitrogen-fixers), which are ultimately at a disadvantage in higher  
431 nutrient environments (Tognetti *et al.*, 2021).

## 432 **Conclusion**

433 Our study examined competing theories of community assembly (HilleRisLambers *et al.*,  
434 2012; Kraft *et al.*, 2015), stability (Connell & Slatyer, 1977; Hallett *et al.*, 2018), and coex-  
435 istence (Tilman, 1985) while informing potential future avenues of theoretical development

436 using community metrics that capture the speed and direction of community change over  
437 time (De Cáceres *et al.*, 2019). Taken together, our results imply that grassland communi-  
438 ties at Cedar Creek tended towards resource-mediated equilibrium states regardless of initial  
439 conditions, but that disturbance made successional pathways more direct. In particular,  
440 disturbance moved successional trajectories towards changes eventually induced by nutrient  
441 addition. Importantly, our results also demonstrated that the rate of community turnover  
442 can remain high as communities approach and reach equilibrium states (Figure 5). As such,  
443 we advocate that future work on succession and community assembly incorporate fluctuation  
444 dependent coexistence and stochastic theory, as communities at their dynamical equilibrium  
445 can be highly variable (Hallett *et al.*, 2019; Shoemaker *et al.*, 2020; Aoyama *et al.*, 2022).

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619 S114–S123.

		Early (1982-1985)		Late (2000-2004)				
Remnant		<i>Poa pratensis</i>	C3					
		<i>Panicum perlongum</i>	C3					
		<i>Panicum oligosanthos</i>	C3					
		<i>Carex spp.</i>	S		<i>Carex spp.</i>	S		
		<i>Ambrosia coronopifolia</i>	F					
		<i>Artemesia ludoviciana</i>	F					
		<i>Rubus sp.</i>	W		<i>Rubus sp.</i>	W		
Intact in 1982		Control		High N		Control		High N
		<i>Schiz. scoparium</i>	C4	<i>Schiz. scoparium</i>	C4	<i>Schiz. scoparium</i>	C4	
				<i>Agropyron repens</i>	C3	<i>Poa pratensis</i>	C3	<i>Agropyron repens</i>
				<i>Panicum oligosanthos</i>	C3			
				<i>Poa pratensis</i>	C3			
				<i>Ambrosia coronopifolia</i>	F			
				<i>Artemesia ludoviciana</i>	F			
Disturbed in 1982		Control		High N		Control		High N
		<i>Setaria lutescens</i>	C4	<i>Setaria lutescens</i>	C4	<i>Schiz. scoparium</i>	C4	
		<i>Panicum oligosanthos</i>	C3	<i>Agropyron repens</i>	C3	<i>Poa pratensis</i>	C3	<i>Agropyron repens</i>
				<i>Panicum oligosanthos</i>	C3			
		<i>Ambrosia coronopifolia</i>	F	<i>Artemesia ludoviciana</i>	F	<i>Lathyrus venosus</i>	L	<i>Rubus sp.</i>
		<i>Artemesia ludoviciana</i>	F	<i>Polygonum convolvulus</i>	F			
		<i>Polygonum convolvulus</i>	F					

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, S = Sedge.

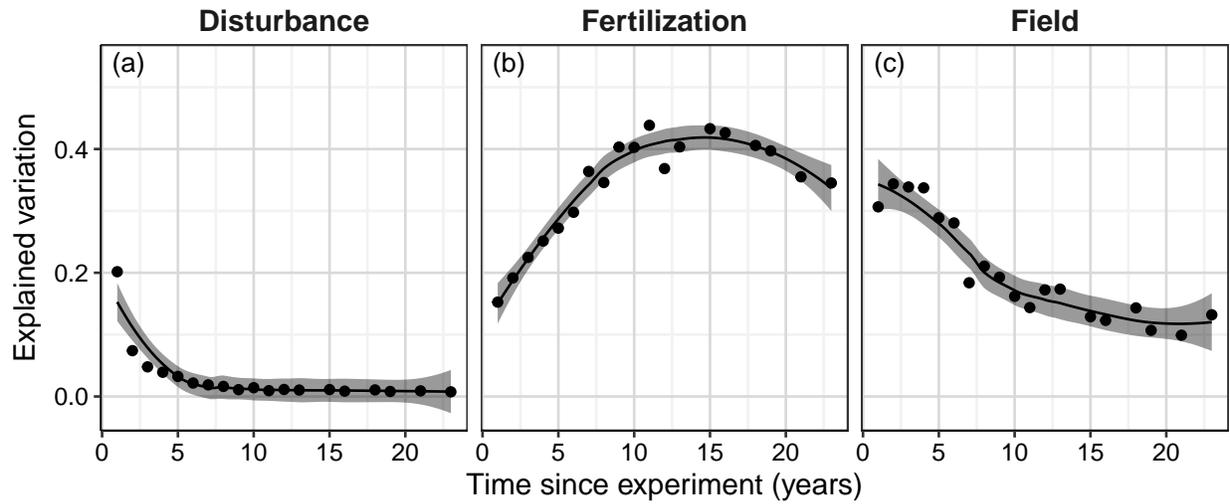


Figure 1: Variation in aboveground plant community composition explained by (a) disturbance (disking event in 1982), (b) annual nutrient addition and (c) field identity (A, B, C) from 1982 to 2004. Plotted values are the  $R^2$  of each independent variable from a PERMANOVA model. Lines represent loess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

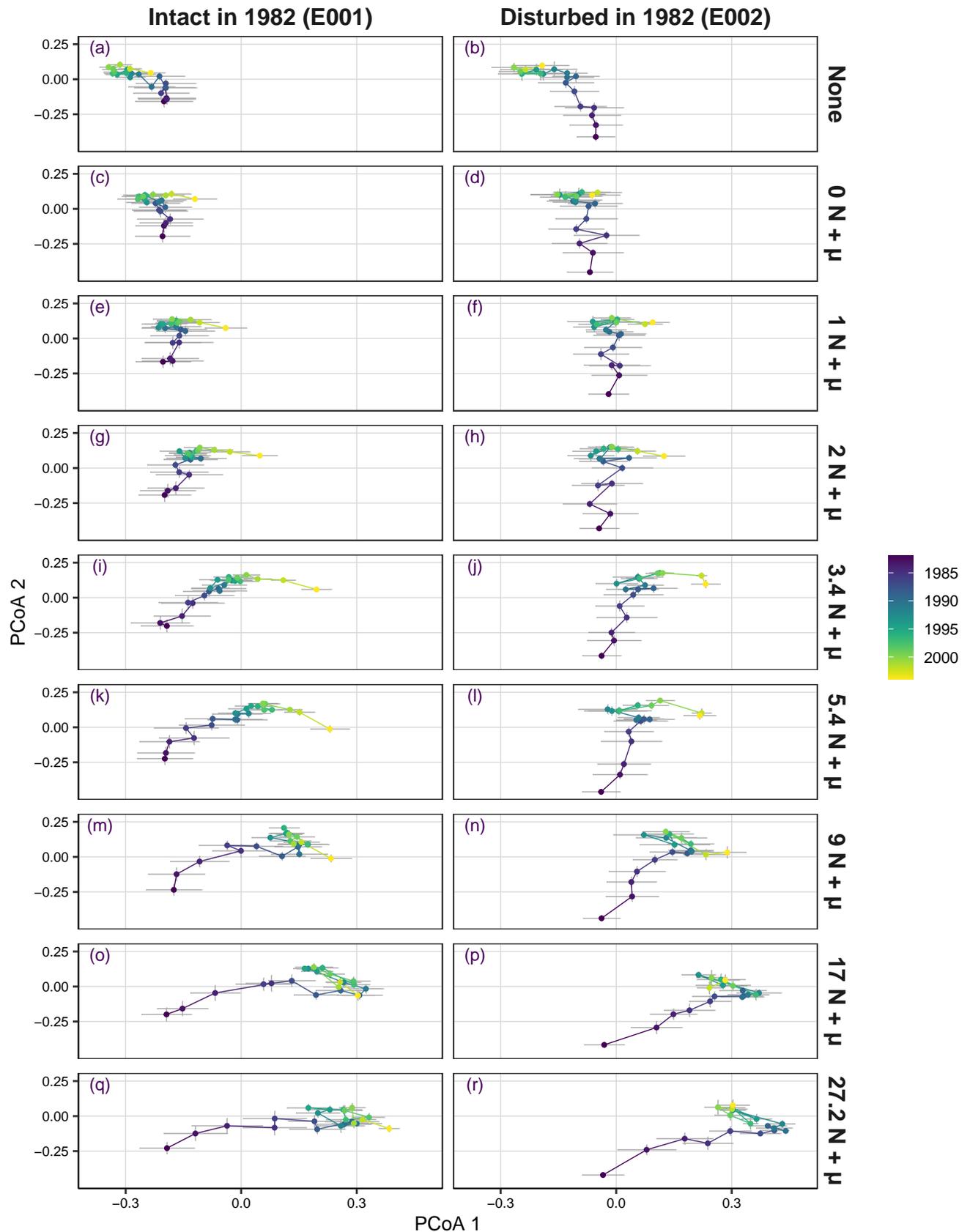


Figure 2: Yearly community trajectories in PCoA ordination space. Points represent mean PCoA scores  $\pm 1$  SE (in gray bars) from aboveground plant community composition data in intact (left column) and disturbed (right column) communities across annual nutrient addition regimes (rows;  $n=18$  for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

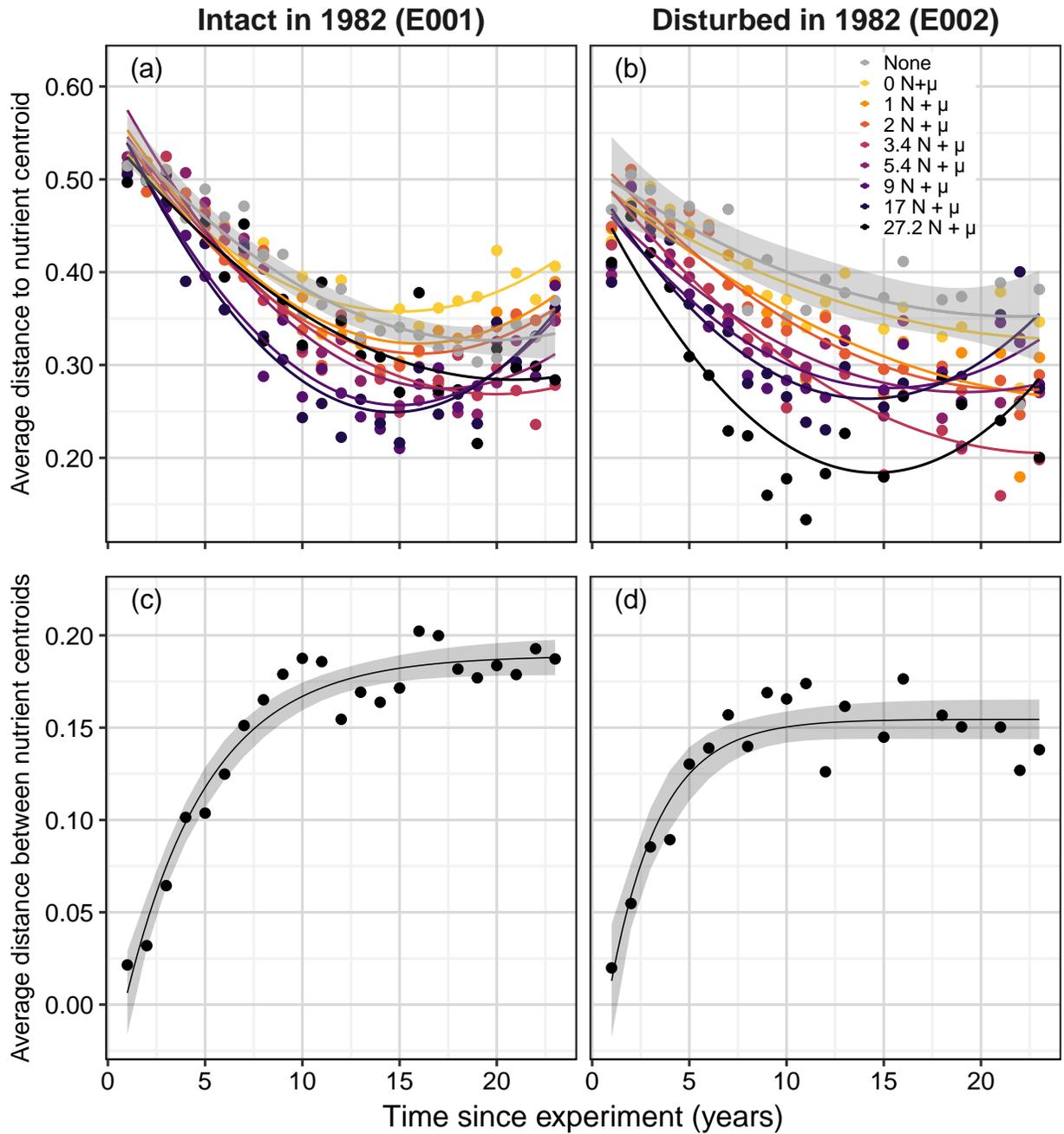


Figure 3: (a & b) Average Bray-Curtis distance from each plot to its nutrient treatment group centroid through time in intact (a) and disturbed plots (b). Lines represent quadratic regressions, with 95% confidence intervals shown for the control. AIC values of competing models and parameter estimates for regressions are in Table 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 Table S3 and S4.

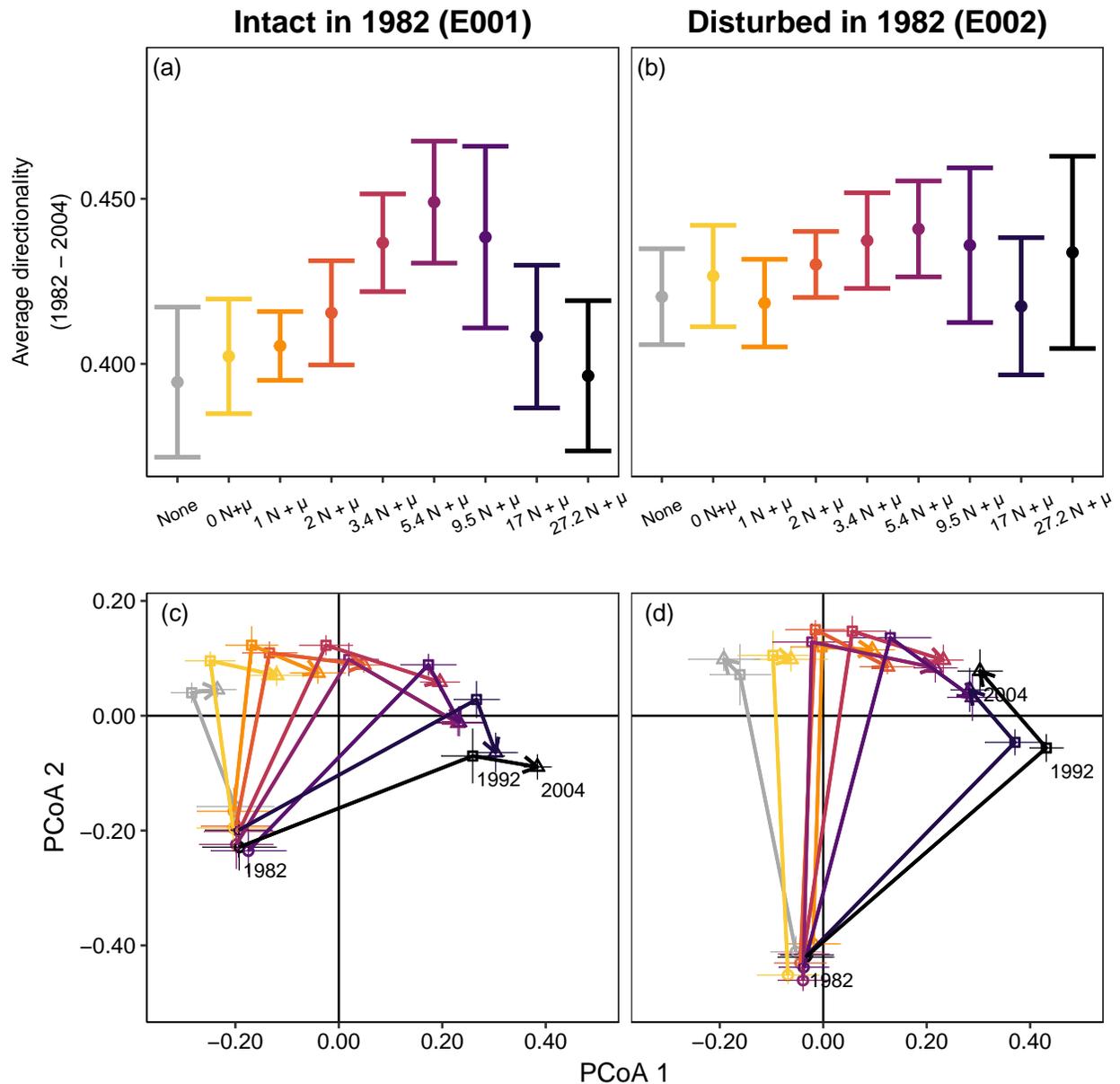


Figure 4: Community trajectories including average directionality (a & b) and decadal trajectories (c & d) in PCoA ordination space in intact (a & c) and disturbed (b & d) communities across different levels of nutrient addition. Low directionality in (a & b) indicate a meandering successional path. Trajectories in c & 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  $\pm 1$  SE (c & d).

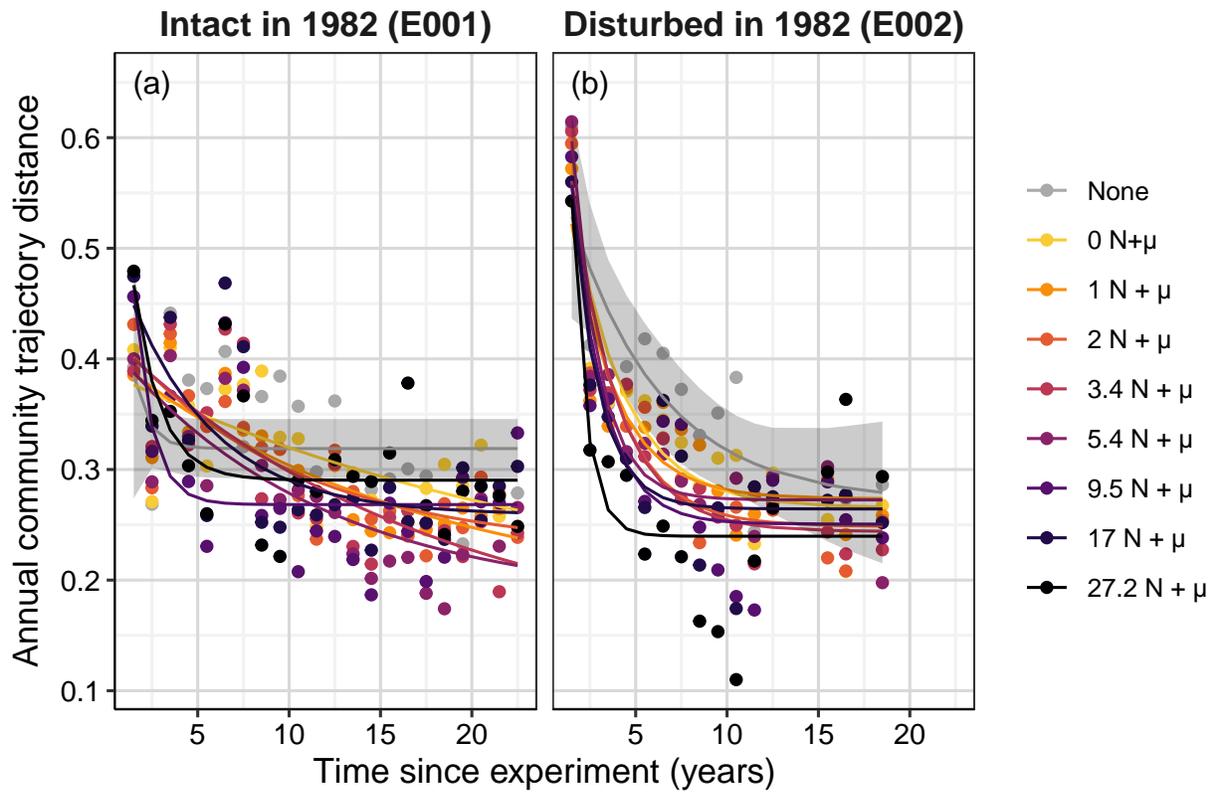


Figure 5: Annual community trajectory distance (temporal species turnover) in aboveground plant community composition in intact (a) and disturbed (b) communities across nutrient addition treatments (colors). Points represent the average trajectory distance between consecutive years of plots with the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