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**Plant community responses to long-term fertilization: Changes in functional group
abundance drive changes in species richness**

Timothy L. Dickson^{1*} and Katherine L. Gross^{1,2}

¹W.K. Kellogg Biological Station, Michigan State University, Hickory Corners, MI 49060, USA

²Department of Plant Biology, Michigan State University, East Lansing, MI 48824, USA

*Present address: Department of Biology, University of Nebraska at Omaha,

Omaha, NE 68182, USA

tdickson@unomaha.edu

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ABSTRACT

Declines in species richness due to fertilization are typically rapid and associated with increases in aboveground production. However, in a long-term experiment examining the impacts of fertilization in an early successional community, we found it took 14 years for plant species richness to significantly decline in fertilized plots, despite fertilization causing a rapid increase in aboveground production. To determine what accounted for this lag in the species richness response, we examined several potential mechanisms. We found evidence suggesting the abundance of one functional group—tall species with long-distance (runner) clonality—drove changes in species richness, and we found little support for other mechanisms. Tall runner species initially increased in abundance due to fertilization, then declined dramatically and were not abundant again until later in the experiment when species richness and the combined biomass of all other functional groups (non-tall runner) declined. Over 86% of the species found throughout the course of our study are non-tall runner, and there is a strong negative relationship between non-tall runner and tall runner biomass throughout our study. We therefore suggest that declines in species richness in the fertilized treatment are due to high tall runner abundance that decreases the abundance and richness of non-tall runner species. By identifying the functional group that drives declines in richness due to fertilization, our results help to elucidate how fertilization decreases plant richness and also suggests that declines in richness due to fertilization can be lessened by controlling the abundance of species with a tall runner growth form.

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INTRODUCTION

Increased fertilization via nitrogen deposition and other inputs is one of the most important factors driving declines in species diversity in terrestrial communities (Clark and Tilman 2008; Sala et al. 2000; Vitousek et al. 1997). A large number of fertilization experiments, particularly in grasslands, show that fertilization decreases plant species richness (DiTommaso and Aarssen 1989; Gough et al. 2000; Suding et al. 2005), especially when fertilization leads to large increases in aboveground biomass production (Suding et al. 2005). Many studies have examined the mechanisms by which fertilization decreases species richness (Dickson and Foster 2011; Eilts et al. 2011), but only a few studies have examined whether particular plant functional groups respond differently to fertilization and drive declines in species richness (Clark et al. 2007; Gough et al. 2012; Suding et al. 2005). One cross-site study that has examined the response of different herbaceous plant functional groups to fertilization finds that fertilization generally increases the abundance of one plant functional group—tall species with long distance (runner) clonality (Gough et al. 2012). Motivated by results reported in Gough et al. (2012), we examined how fertilization affects the abundance of different functional groups in a long-term fertilization experiment. Specifically, we investigated whether increases in tall runner abundance in response to fertilization could explain declines in species richness and the abundance of other functional groups over time, and we also examined a number of other alternate hypotheses.

If increases in the abundance of one functional group result in decreases in the abundance of other functional groups, this should lead to the declines in species evenness often observed after fertilization (Collins et al. 2008; Kempton 1979; Turkington et al. 2002). A meta-analysis by Hillebrand et al. (2007) found that fertilization can have no effect or even lead to

64 slight increases in species richness if no species dominate the community (high species
65 evenness). Hillebrand et al. (2007) also point out that herbivory can reduce the negative effects
66 of fertilization on species richness if herbivory decreases plant dominance. We sought to go
67 beyond an examination of how fertilization impacts community-level relative abundance and
68 explore how changes in the abundance of particular functional groups drive changes in diversity
69 following fertilization.

70 Here we present results from the first 23-years of an ongoing nitrogen addition
71 experiment conducted in a set of replicate successional old-field plant communities at the Long
72 Term Ecological Research project at the W.K. Kellogg Biological Station in southwestern
73 Michigan. Fertilization did not significantly impact species richness until 14 years into the
74 experiment (Gough et al. 2000; Huberty et al. 1998), despite a significant increase in above-
75 ground production. This lag in effect of fertilization on species richness provided an opportunity
76 to examine how fertilization interacts with changes in species composition and functional group
77 abundance to affect species richness.

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MATERIALS AND METHODS

80 This experiment was conducted at Michigan State University's W.K. Kellogg Biological
81 Station (KBS), at the Long Term Ecological Research (LTER) site in agricultural ecology in
82 southwestern Michigan, USA (42°24' N latitude, 85°22' W longitude). Soils at this site are
83 Typic Hapludalfs, either fine-loamy, mixed, mesic Kalamazoo series or coarse-loamy, mixed,
84 mesic Oshtemo series (Mokma and Doolittle 1993). Temperatures range from an average
85 monthly high of 30°C in July to an average monthly low of -8°C in January. Precipitation (\approx

86 1000mm annually) is spread fairly evenly throughout the year with somewhat less precipitation
87 falling in the winter than other seasons.

88 The experiment was established in 1989 in six replicate plots (each 105 m x 87 m) of the
89 successional treatment of the KBS LTER. Replicate fields were plowed in the spring following
90 20 + years of continuous corn production, and natural succession was then allowed to occur with
91 occasional prescribed burns (see below). Succession led to herbaceous vegetation dominated by
92 *Solidago* (goldenrod) species (*S. altissima* and *S. graminifolia*), and to a lesser extent by
93 *Apocynum cannabinum* (dogbane), and *Elymus repens* (quackgrass)—all tall, highly clonal
94 species (Huberty et al. 1998). Two 5 m x 5 m subplots were established in the north end of each
95 plot and one of the subplots was fertilized with 12 g N m⁻² in early summer (typically mid-June),
96 corresponding to the timing of fertilizer application in the surrounding row-crop treatment of the
97 LTER. Fertilizer was added as ammonium nitrate pellets. Information about soil nitrogen levels
98 throughout the experiment can be found in Fig. S1. Further information about the site and the
99 experiment can be found in Huberty et al. (1998) and Grman et al. (2010).

100 Plant species composition and biomass was determined annually from both the fertilized
101 and unfertilized (control) subplots. To avoid edge effects, harvested quadrats were located in the
102 central (3 m x 3 m area) of the subplot; the location of the harvested quadrat was shifted each
103 year so that harvested areas were not resampled for 5 years. Harvests were completed at peak
104 biomass (typically early August) and all vegetation rooted in the harvested quadrat was clipped
105 at ground level. Harvested biomass was separated into live and dead biomass; live biomass was
106 separated by species, dried at 60°C to constant weight, and weighed with 0.01 g accuracy.
107 Species richness and abundance were calculated from the harvested live biomass. In the first
108 three years of the study (1989-1991), the area of the harvested quadrat varied (0.2 m² in 1989 and

109 0.3 m² in 1990-1991), but since 1992 the quadrat has been standardized at 1 m² (0.5 m x 2 m).
110 We show the effects of fertilization on species richness for all years (Fig. 1), but only use data
111 from 1992 onwards for all other analyses.

112 We classified species into three height groups based on their position in the canopy (top
113 third = tall, middle third = mid, bottom third = short) and three clonal growth form groups
114 (runners = species with a spreading morphology that can send up new shoots some distance from
115 the original clone; clumpers = species which produce shoots adjacent to the original clone, non-
116 clonal = species that do not spread) by utilizing height and clonality information in McGregor et
117 al. (1986) and through personal observations of species' height (a species could have the
118 potential to grow taller at some locations in its range rather than at our site). This classification
119 is similar to that used by Gough et al. (2012) and Cleland et al. (2008), except that we have
120 differentiated between mid and tall canopy species in our analysis.

121 **Site Management:** Woody species began to invade the site a few years after the start of
122 the experiment (Foster and Gross 1999), and by 1997 trees like *Robinia pseudoacacia* (black
123 locust) and *Rhus typhina* (stag horn sumac) became common in some replicates. Because the
124 intent of this successional treatment was to provide an herbaceous-dominated reference
125 community for comparison with the crop treatments on the KBS LTER, management was
126 initiated to remove woody invaders from these plots and prevent reinvasion. This included
127 initiation of whole-plot annual prescribed burning in 1997 (spring) to control further colonization
128 by woody species and cutting and removing woody stems. Details of the management of these
129 fields can be found at (<http://lter.kbs.msu.edu/>). We did not find that species richness or the
130 effect of fertilization on species richness was significantly affected by burning (Fig. S2).

131 **Statistical Analysis:** All statistical analyses were completed using PROC MIXED in
132 SAS 9.2 (Cary, NC, USA). We sought to determine how the effects of fertilization on plant
133 species richness and the biomass of different functional groups varied through time, and whether
134 the biomass of tall runner and non-tall runner species could help to explain the changes in plant
135 species richness over time. Therefore, we performed split-plot, repeated-measure Analysis of
136 Variance (RM-ANOVA) for analyses, except where a covariate such as tall runner biomass or
137 non-tall runner biomass was included in which case we performed split-plot, repeated-measure
138 Analysis of Covariance (RM-ANCOVA). We used a Kenward-Rogers correction in all analyses,
139 which led to reduced degrees of freedom and to decimals in the degrees of freedom due to
140 missing data (biomass was not collected from one quadrat in 1997).

141 We tested the data for normality and transformed the data if necessary to improve
142 normality (data are transformed in figures in these cases). We treated each plot as a separate
143 block. The blocking term was added as a random effect to all analyses to remove any effects of
144 spatial variation and is not reported.

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RESULTS

147 Over the first 13 years of the experiment (1989-2001), fertilization did not significantly
148 affect plant species richness (Fig. 1), despite the fact that fertilization significantly increased total
149 biomass by 64% during this period (Fig. 2A). In 2002, 14 years after the fertilization treatment
150 was initiated, species richness significantly declined in the fertilized plots and remained lower
151 most years thereafter (Fig. 1; year x fertilizer interaction). We set out to determine why
152 fertilization did not decrease species richness until 2002, even though total biomass was quickly
153 increased by fertilization.

154 The observed decline in species richness in fertilized plots occurred when fertilization led
155 to a sustained increase in the abundance of species with a tall runner growth form. Tall runner
156 biomass initially increased due to fertilization, then declined sharply in 1995, and then showed a
157 sustained increase at the same time species richness declined (Fig. 2B). Two species in the
158 genus *Solidago* (*S. altissima* and *S. graminifolia*) made up most of the tall runner biomass in the
159 fertilized treatment in the first part of the experiment (1989-2001). In the latter part of the
160 experiment (2002-2011) when tall-runners again dominated the fertilized plots, *Solidago* species
161 were again abundant, but made up less of the tall runner biomass (Fig. 2B). The biomass of all
162 other functional groups (non-tall runners) was not significantly affected by fertilization until
163 2005, but was significantly decreased by fertilization in most years from 2005 onwards (Fig.
164 2C). The timing of the decline in biomass of these other functional groups generally
165 corresponded to when we observed a significant decline in species richness (Fig.1). The change
166 in the relative abundance of tall runners in response to fertilization can also be clearly seen when
167 examining the percent of total biomass made up of tall runner species over the course of the
168 experiment (Fig 2D). No functional group other than tall runners increased in biomass in
169 response to fertilization (Fig. S3).

170 It appears fertilization decreased species richness when tall runner biomass remained
171 high for long enough to lead to decreases in non-tall runner biomass. Specifically, there was a
172 significant negative relationship between tall runner biomass and non-tall runner biomass (Fig
173 3A). Over 86% of species observed from 1992 onwards had a non-tall runner growth form,
174 which helps to explain why species richness declined when tall runner biomass increased—and
175 non-tall runner biomass decreased. There was a significant positive relationship between non-
176 tall runner biomass and species richness (Fig. 3B), and a significant negative relationship

177 between tall runner biomass and species richness (Fig. 3C; note that the fertilization term in the
178 model is not significant when tall runner biomass is included as a covariate). The biomass of no
179 other functional group or species accounted for these observed changes in species richness (Fig.
180 S3-S4). Also, the relationship between total biomass and species richness was only weakly
181 significant (Fig. 3D), suggesting that changes in the biomass of the tall runner and non-tall
182 runner functional groups were driving changes in richness rather than changes in total biomass.

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DISCUSSION

185 While declines in species richness are commonly observed in response to fertilization in
186 grasslands (Clark et al. 2007; Suding et al. 2005), typically these responses occur quickly and are
187 correlated with increases in community biomass (Suding et al. 2005). We are not aware of any
188 other study that has documented such a long-term temporal lag (14 years) in the species richness
189 response to fertilization when there is a strong fertilization effect on above-ground production.
190 The magnitude of the total biomass response to fertilization does not appear to provide a
191 sufficient explanation as to why it took 14 years for species richness to decline in this
192 experiment. Specifically, total biomass in the fertilized treatment was significantly higher than
193 the unfertilized treatment in most years of the experiment, except drought years, as suggested by
194 the significant effect of fertilization and the non-significant year x fertilizer interaction (Fig. 2A).
195 Also, the effects of fertilizer on total biomass in our study were similar in magnitude to other
196 fertilization experiments (Gough et al. 2012).

197 Instead, we found that increases in the biomass of a particular functional group—species
198 with a tall runner growth form—rather than increases in total biomass, appeared to drive declines
199 in species richness by decreasing the average biomass of the 86% of species that are not tall

200 runner. Gough et al. (2012) also found that the tall runner functional group consistently
201 increased in abundance in response to fertilization across 37 experiments in North American
202 grasslands. Interestingly, Gough et al. (2012) found a consistent response of the tall runner
203 functional group across many locations, but the response was generally driven by a single—but
204 different—species at each location. The response at our site was primarily driven by *Solidago*
205 species, primarily *S. altissima*. *Solidago* species made up much of the tall runner biomass, and
206 provided almost as good a fit to species richness as did tall runner biomass (Fig. S5). However,
207 we focus on tall runner species because they provide the strongest fit with species richness (Fig.
208 S5) and because of the generality of their response to fertilization across sites (Gough et al.
209 2012).

210 The Gough et al. (2012) study did not find a significant relationship between species
211 richness and the response of tall runner species to fertilization, but they noted that the relative
212 abundance ratios used in their analyses may have masked such a relationship. In addition, the
213 Gough et al. (2012) meta-analysis used data from only one year of each of the 37 experiments
214 (last year of data available from each site in Cleland et al. 2008 data set). This would also have
215 masked the relationship between tall runner species and richness (ex. used the 2001 data from
216 our study, in which fertilization did not significantly decrease richness). Our results thus expand
217 upon Gough et al. (2012) by examining the effects of tall runner species through time and by
218 using analyses that reveal how changes in functional group abundance over time can drive
219 community responses to fertilization.

220 The observation that tall runner biomass appeared to drive changes in species richness
221 raises two obvious, but difficult to answer questions: 1) Why did the initial spike in tall runner
222 biomass in the first part of the experiment not cause a decrease in species richness?; and 2) What

223 caused the precipitous decline in abundance of tall runner species in the fertilized treatment in
224 1995? The answer to the first question may be that high tall runner biomass was not sustained
225 for long enough in the first part of the experiment to decrease non-tall runner biomass and
226 species richness. Transient dynamics can occur whereby inferior competitors persist until
227 resource levels equilibrate (Tilman 1988) or disturbance ceases (Huston 1979). We suggest that
228 one year of high tall runner biomass in 1994 was not enough to exclude many species—figure
229 2C shows that non-tall runner biomass decreased in 1994 as tall runner biomass reached its
230 maximum, but then recovered in 1995 when tall runner biomass declined.

231 The answer to the second question requires a bit more speculation and inference from
232 other experiments that have examined the impacts of insect herbivores on plant communities and
233 how this varies in response to fertilization. Most of the tall-runner biomass at the beginning of
234 the experiment was composed of *Solidago* species; in the fertilized treatment *S. altissima* and *S.*
235 *graminifolia* made up over 85% of the tall-runner biomass and 65% of the total biomass from
236 1992-1994. These are both native species that are vulnerable to predation by insect herbivores
237 (Carson and Root 1999), and we suggest a *Solidago*-specific insect herbivore may have
238 decreased *Solidago* biomass in 1995. Work by Carson and Root (2000) provides a good example
239 of how this could occur—in their study an outbreak of a *Solidago*-specific insect herbivore
240 (*Microrhopala vittata*) strongly reduced *Solidago* abundance for several years relative to insect
241 exclusion treatments and led to increases in plant species richness. Other studies have shown
242 that a variety of insect herbivores (including insects in the *Trirhabda* genus) can strongly reduce
243 *Solidago* abundance (Carson and Root 1999; Maddox and Root 1990). Although we have no
244 direct evidence of a 1995 insect outbreak, *Trirhabda* species were observed in the plots during
245 this time (Katherine Gross personal observations). It has also been shown that insects often

246 preferentially feed on fertilized vegetation (Uriarte 2000), which may help to explain why the
247 decline in *Solidago* biomass was so large in the fertilized treatment. More broadly, grazing by
248 small mammals has also been shown to reduce the negative effects of fertilization on plant
249 species richness (Gough and Grace 1998; Inouye et al. 1987). Regardless of what accounts for
250 the rapid decline and delayed re-establishment of tall runner species in this system, our results
251 suggest that changes in tall runner abundance related to fertilization are an important driver of
252 declines in plant species richness following fertilization.

253

254 **Other potential hypotheses**

255 We explored whether other hypotheses beyond the abundance of tall runner species could
256 explain both the magnitude and the delay of the species richness response in our study.
257 However, we could not find support for any other explanations. Fire has been shown to be an
258 important driver of plant biomass and species richness in tall-grass prairie (Collins et al. 1998).
259 In our experiment, fire was introduced in 1997 to control woody species invasion, and while we
260 do not have unburned control plots, we find no evidence that fire drove changes in species
261 richness (Fig. S2). Similarly, increased litter biomass in response to fertilization has been shown
262 to be an important limit on species richness in grasslands (Foster and Gross 1998). We examined
263 whether litter biomass was correlated with species richness in our study, but found no significant
264 relationship (Fig. S6). We also examined whether the abundance of other functional groups (ex.
265 legumes, grasses) could explain changes in species richness over time, but found little support
266 for other functional groups driving changes in richness over time (Fig. S4). Lastly, fertilization
267 has been shown to alter colonization rates (Tilman 1993), which could be important in our

268 successional fields (Huberty et al. 1998). However, fertilization had little effect on species
269 colonization rates (gain or loss of species) in our study (Fig. S7).

270 While other factors may have contributed to the lag in effects of fertilization on species
271 richness, it seems that the consistent increase in tall runner biomass in the latter part of the
272 experiment and the associated decrease in non-tall runner biomass is the most parsimonious
273 explanation for this lag. However, as with every time series experiments, we cannot rule out the
274 possibility of unmeasured variables affecting plant species richness over time and future
275 experiments should be completed to isolate the effects of tall runner biomass on species richness.

276

277 **General relevance**

278 The results of our study provide insights to understanding the responses of plant
279 communities to long term perturbations. We have shown that particular functional groups can
280 play an important role in controlling plant species richness under fertilized conditions, and we
281 discuss below how this may be important when managing sites with high soil fertility for high
282 plant diversity. While other studies have shown that species dominance can be a driver of
283 diversity (Hillebrand et al. 2007), the role of particular functional groups in controlling richness
284 under fertilized conditions is less well understood. For example, Clark et al. (2007) presented
285 evidence that sites with higher C₄ graminoid abundance showed strong responses to fertilization
286 and this correlated with greater species diversity loss. Although the abundance of C₄ graminoid
287 species was initially high in our study, this functional group rapidly declined in abundance (Fig.
288 S4), and the abundance of this functional group did not correspond to changes in species richness
289 in response to fertilization. Suding et al. (2005) presented evidence that greater shifts in
290 abundance of functional groups was correlated with greater species losses, and they also did not

291 find C₄ graminoids were important in determining species losses. Instead, they found that
292 legumes were the most likely functional group to be lost due to fertilization. We also found that
293 legume species were lost in the fertilized treatment, but this only explained a small amount of
294 total species losses due to fertilization. We suggest that height and clonality functional groups
295 provide greater predictive power for the effects of fertilization on plant species richness than do
296 growth form (graminoid, non-leguminous forb, leguminous forb) or photosynthetic pathway (C₄
297 and C₃) functional groups.

298 Few studies have considered how to prevent species losses under fertilized conditions
299 (but see Collins et al. 1998, Foster et al. 2010, Symstad and Jonas 2011). The studies that have
300 considered how to prevent losses in species richness have generally focused on the role of
301 disturbance in preventing losses. Disturbances such as grazing or haying have been shown to
302 increase plant diversity under high productivity conditions (Collins et al. 1998; Foster et al.
303 2010; Hillebrand et al. 2007; Symstad and Jonas 2011), but these studies give little detail on the
304 mechanisms by which disturbances increase plant diversity. Understanding these mechanisms
305 will become increasingly important if grasslands are increasingly fertilized and disturbed as part
306 of cellulosic biofuel production (Gelfand et al. 2013).

307 Disturbances may help to prevent losses of species due to fertilization because
308 fertilization increases the abundance of dominant species (Turkington et al. 2002; Collins et al.
309 2008; Fig. S8), and disturbance may decrease the abundance of dominant species (Hillebrand et
310 al. 2007). A meta-analysis across many studies shows that fertilization only decreases species
311 richness when a few species are highly abundant and evenness is low (Hillebrand et al. 2007).
312 These results are similar to our finding of a negative relationship between tall runner and non-tall
313 runner biomass and of plant species richness not declining until sustained increases occur in tall

314 runner biomass. There are several studies that suggest removing dominant (Gurevitch and
315 Unnasch 1989) or clonal species (Eilts et al. 2011; Reynolds et al. 2007) generally removes the
316 negative effects of fertilization on species richness. In contrast, Lepš (1999) found that removal
317 of dominant species does not necessarily prevent a decrease in species richness after fertilization,
318 although other species increased in abundance after dominant removal in this study and may
319 have filled the role of dominant competitors. If fertilization is primarily acting by increasing the
320 abundance of dominant species which thereby reduces the abundance of subdominant species,
321 then future research should examine how changes in the abundance of dominant and
322 subdominant species affect species richness rather than how changes in total biomass affect
323 species richness.

324 The mechanisms by which highly abundant species decrease plant richness under
325 fertilized conditions also need to be determined. One might expect that increases in the
326 abundance of dominant species would decrease light levels and thereby lead to decreases in the
327 abundance of non-tall runner species. Light manipulation experiments in the presence and
328 absence of tall runner species would be necessary to fully address the role of light competition.
329 However, we suggest that all tall-statured species—not just tall runner species—would increase
330 in abundance under fertilized conditions if light competition was the only factor causing changes
331 in functional group biomass. We found fertilization decreased or had no effect on the biomass of
332 tall-statured species without the runner growth form (Fig. S3), suggesting that plants competed
333 for additional resources beyond light (see also Dickson and Foster 2011).

334

335 **Conclusions**

336 Overall, our results suggest that fertilization decreases plant richness by increasing the
337 abundance of tall runner species and thereby decreasing the abundance of other functional
338 groups. Other than Gough et al. (2012), the effects of fertilization on tall runner biomass has not
339 been examined, and future studies should examine the role of tall runner species in driving
340 declines in plant richness in other habitats.

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342

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REFERENCES

349 Carson WP, Root RB (2000) Herbivory and plant species coexistence: Community regulation by
350 an outbreaking phytophagous insect. *Ecological Monographs* 70:73–99.

351 Carson WP, Root RB (1999) Top-down effects of insect herbivores during early succession:
352 influence on biomass and plant dominance. *Oecologia* 121:260–272.

353 Clark CM, Cleland EE, Collins SL, et al. (2007) Environmental and plant community
354 determinants of species loss following nitrogen enrichment. *Ecology letters* 10:596–607.

355 Clark CM, Tilman D (2008) Loss of plant species after chronic low-level nitrogen deposition to
356 prairie grasslands. *Nature* 451:712–715.

357 Cleland EE, Clark CM, Collins SL, et al. (2008) Species responses to nitrogen fertilization in
358 herbaceous plant communities, and associated species traits. *Ecology* 89:1175.

359 Collins SL, Knapp AK, Briggs JM, et al. (1998) Modulation of diversity by grazing and mowing
360 in native tallgrass prairie. *Science* 280:745–747.

361 Collins SL, Suding KN, Cleland EE, et al. (2008) Rank Clocks and Plant Community Dynamics.
362 *Ecology* 89:3534–3541.

363 Dickson TL, Foster BL (2011) Fertilization decreases plant biodiversity even when light is not
364 limiting. *Ecology letters* 14:380–8.

365 DiTommaso A, Aarssen LW (1989) Resource manipulations in natural vegetations: a review.
366 *Vegetatio* 84:9–29.

- 367 Eilts JA, Mittelbach GG, Reynolds HL, Gross KL (2011) Resource Heterogeneity, Soil Fertility,
368 and Species Diversity: Effects of Clonal Species on Plant Communities. *The American*
369 *naturalist* 177:574–588.
- 370 Foster BL, Gross KL (1998) Species richness in a successional grassland: Effects of nitrogen
371 enrichment and plant litter. *Ecology* 79:2593–2602.
- 372 Foster BL, Gross KL (1999) Temporal and Spatial Patterns of Woody Plant Establishment in
373 Michigan Old Fields. *The American Midland Naturalist* 142:229–243.
- 374 Foster BL, Khavin IS, Murphy CA, et al. (2010) Integrated responses of grassland biodiversity
375 and ecosystem properties to hay management: A field experiment. *Transactions of the*
376 *Kansas Academy of Science* 113:103–119.
- 377 Gelfand I, Sahajpal R, Zhang X, et al. (2013) Sustainable bioenergy production from marginal
378 lands in the US Midwest. *Nature* 493:514–517.
- 379 Gough L, Grace JB (1998) Herbivore effects on plant species density at varying productivity
380 levels. *Ecology* 79:1586–1594.
- 381 Gough L, Gross KL, Cleland EE, et al. (2012) Incorporating clonal growth form clarifies the role
382 of plant height in response to nitrogen addition. *Oecologia* 169:1053–1062.
- 383 Gough L, Osenberg CW, Gross KL, Collins SL (2000) Fertilization effects on species density
384 and primary productivity in herbaceous plant communities. *Oikos* 89:428–439.

- 385 Grman E, Lau JA, Schoolmaster DR, Gross KL (2010) Mechanisms contributing to stability in
386 ecosystem function depend on the environmental context. *Ecology letters* 13:1400–10.
- 387 Gurevitch J, Unnasch RS (1989) Experimental removal of a dominant species at two levels of
388 soil fertility. *Canadian Journal of Botany* 67:3470–3477.
- 389 Hillebrand H, Gruner DS, Borer ET, et al. (2007) Consumer versus resource control of producer
390 diversity depends on ecosystem type and producer community structure. *Proceedings of the*
391 *National Academy of Sciences of the United States of America* 104:10904–10909.
- 392 Huberty LE, Gross KL, Miller CJ (1998) Effects of nitrogen addition on successional dynamics
393 and species diversity in Michigan old-fields. *Journal of Ecology* 86:794–803.
- 394 Huston M (1979) A general hypothesis of species diversity. *The American Naturalist* 113:81–
395 101.
- 396 Inouye RS, Huntly NJ, Tilman D, Tester JR (1987) Pocket gophers (*Geomys bursarius*),
397 vegetation, and soil nitrogen along a successional sere in east-central Minnesota. *Oecologia*
398 72:178–184.
- 399 Kempton RA (1979) The Structure of Species Abundance and Measurement of Diversity.
400 *Biometrics* 35:307–321.
- 401 Lepš J (1999) Nutrient status, disturbance and competition: an experimental test of relationships
402 in a wet meadow. *Journal of Vegetation Science* 10:219–230.

- 403 Maddox GD, Root RB (1990) Structure of the Encounter between Goldenrod (*Solidago*
404 *altissima*) and Its Diverse Insect Fauna. *Ecology* 71:2115.
- 405 McGregor RL, Barkley TM, Brooks RE, Schofield EK (1986) *Flora of the Great Plains*.
406 University Press of Kansas, Lawrence, Kansas
- 407 Mokma DL, Doolittle JA (1993) Mapping soils and soil properties in southwest Michigan using
408 ground-penetrating radar. *Soil survey horizons* 34:13–22.
- 409 Reynolds HL, Mittelbach GG, Darcy-Hall TL, et al. (2007) No effect of varying soil resource
410 heterogeneity on plant species richness in a low fertility grassland. *Journal of Ecology*
411 95:723–733.
- 412 Sala OE, III FSC, Armesto JJ, et al. (2000) Global biodiversity scenarios for the year 2100.
413 *Science* 287:1770–1774.
- 414 Suding KN, Collins SL, Gough L, et al. (2005) Functional- and abundance-based mechanisms
415 explain diversity loss due to N fertilization. *Proceedings of the National Academy of*
416 *Sciences of the United States of America* 102:4387–92.
- 417 Symstad AJ, Jonas JL (2011) Incorporating Biodiversity Into Rangeland Health: Plant Species
418 Richness and Diversity in Great Plains Grasslands. *Rangeland Ecology & Management*
419 64:555–572.
- 420 Tilman D (1988) *Plant Strategies and the Dynamics and Structure of Plant Communities*.
421 Princeton University Press, Princeton, N.J.

- 422 Tilman D (1993) Species richness of experimental productivity gradients: How important is
423 colonization limitation. *Ecology* 74:2179–2191.
- 424 Turkington R, John E, Watson S, Seccombe-Hett P (2002) The effects of fertilization and
425 herbivory on the herbaceous vegetation of the boreal forest in north-western Canada: a 10-
426 year study. *Journal of Ecology* 90:325–337.
- 427 Uriarte M (2000) Interactions between goldenrod (*Solidago altissima* L.) and its insect herbivore
428 (*Trirhabda virgata*) over the course of succession. *Oecologia* 122:521–528.
- 429 Vitousek PM, Aber JD, Howarth RW, et al. (1997) Human alteration of the global nitrogen
430 cycle: Sources and consequences. *Ecological Applications* 7:737–750.
- 431

432

FIGURE LEGENDS

433 Figure 1. Effects of fertilization and year on plant species richness (species richness refers to the
434 number of species per sample area; sample area was less than 1 m² in first three years and 1 m²
435 from 1992 onwards, see Methods for details; values are means \pm 1 SE; N=6).

436

437 Figure 2. Effects of fertilization and year on (A) total community biomass, (B) biomass of tall
438 runner species and *Solidago* species, (C) biomass of all species other than tall runner species, and
439 (D) percentage of total biomass made up of tall runner species (values are mean \pm 1 SE; N=6).

440

441 Figure 3. The relationship between (A) tall runner biomass and the biomass of all other species,
442 (B) the biomass of non-tall runner species and plant species richness, (C) tall runner biomass and
443 plant species richness, and (D) total biomass and plant species richness (note that non-tall runner
444 biomass is on a square root scale).

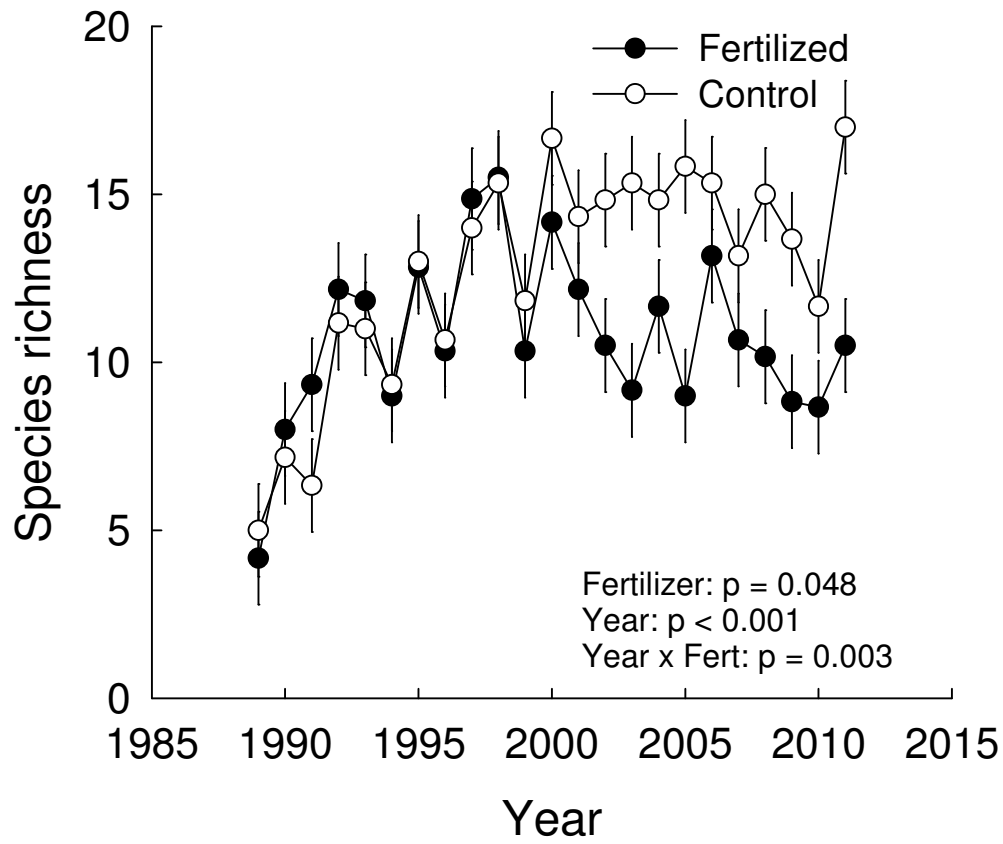


Figure 1.

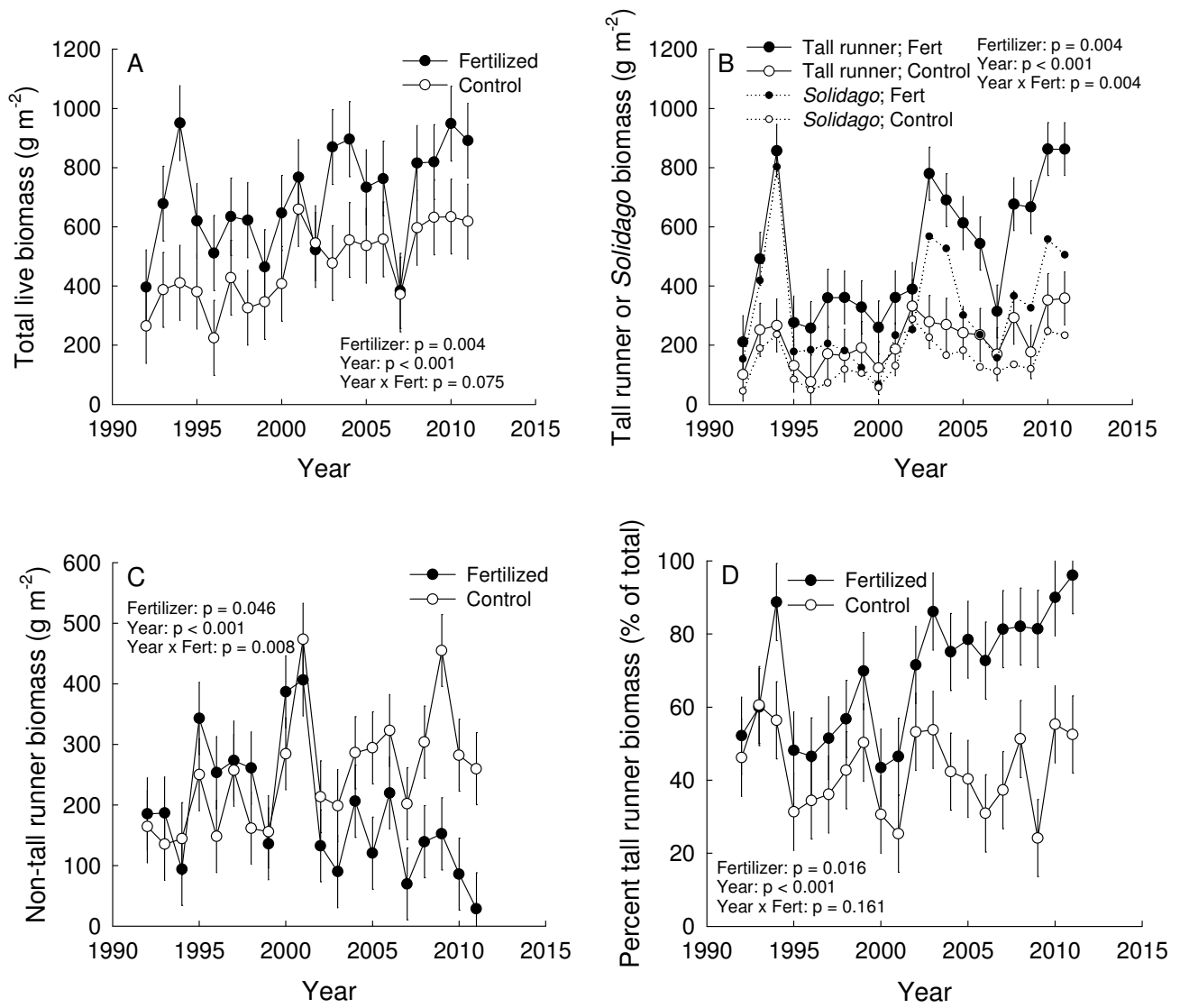


Figure 2.

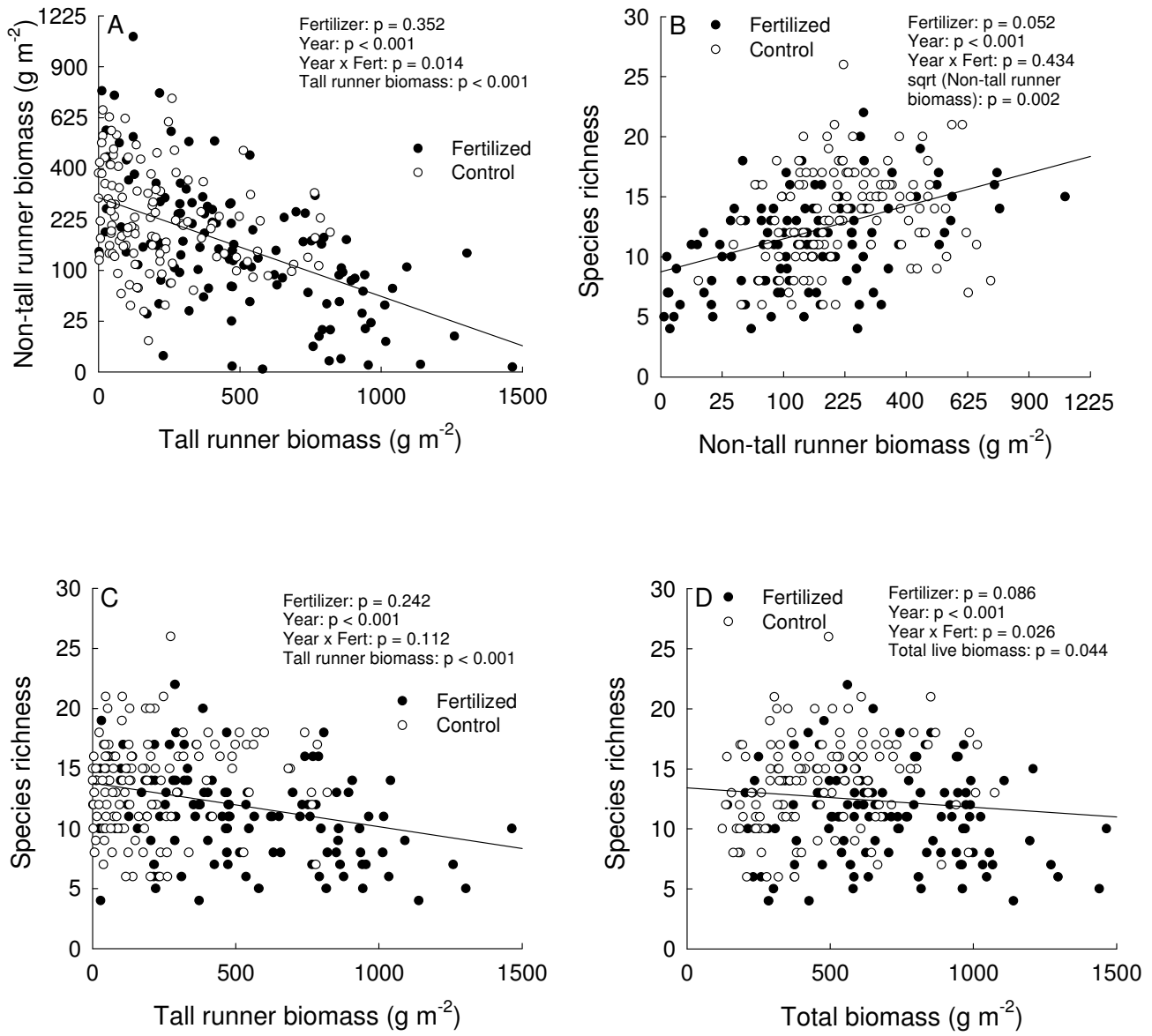


Figure 3.