

1 **Does multiple nutrient enrichment impact the stability of grassland biomass**
2 **production?**

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76 **ABSTRACT**

77 Nutrient enrichment can simultaneously increase and destabilize plant biomass production, with
78 co-limitation by multiple nutrients potentially influencing these effects. Here, we test how
79 factorial additions of nitrogen (N), phosphorus (P), and potassium with essential nutrients (K+)
80 affect the stability (mean/standard deviation) of aboveground biomass in 34 grasslands over
81 seven years. Destabilization with fertilization was prevalent and was largely driven by single
82 nutrients, rather than synergistic nutrient interactions. N-based treatments increased mean
83 production by 21-51% but increased temporal variability by 40-68% and so consistently reduced
84 stability. P alone increased variability and instability without altering mean biomass, while K+ had
85 no general effects. Declines in stability were largest in the most nutrient-limited grasslands, or
86 where nutrients reduced species richness or intensified species synchrony. We show that adding
87 limiting nutrients can differentially impact mean-variability proportionality and that N and P in
88 particular magnify fluctuations in inter-annual productivity, even if biomass continues to
89 increase.

90

91 **INTRODUCTION**

92 Biomass production is a critical ecosystem function that supports services such as carbon storage
93 and food supply (Kremen 2005; Cardinale *et al.* 2012; Gounand *et al.* 2020). Consequently,
94 understanding how global changes impact the rate and stability of ecosystem biomass
95 production – i.e. the ratio of the temporal mean of biomass production to its temporal standard
96 deviation ($S = \mu/\sigma$; Tilman 1999; Tilman *et al.* 2006) - is an important undertaking (Koerner *et al.*
97 2016; Avolio *et al.* 2020). Terrestrial biomass may be limited by the availability of a single resource
98 like water (Huxman *et al.* 2004; Morgan *et al.* 2016), nitrogen (N; LeBauer & Treseder 2008), or
99 phosphorus (P; Hou *et al.* 2020), or co-limited by multiple resources that interactively affect
100 production (Elser *et al.* 2007; Harpole *et al.* 2011; Fay *et al.* 2015; Kaspari & Powers 2016).
101 Accordingly, pervasive human-driven alterations of nutrient availability can strongly affect rates
102 of biomass production and associated ecosystem services (Tilman 2001; Tilman & Lehman 2001).
103 Nutrient enrichment can also destabilize biomass production over time by altering community
104 attributes that contribute to its stability, such as species richness and synchrony (Hautier *et al.*
105 2014, 2020; McCann *et al.* 2021). However, while the co-limitation of biomass production by
106 multiple nutrients is well demonstrated, we lack understanding of the independent and
107 interactive effects of different nutrients on its temporal stability.

108 Processes operating among individuals, populations, and communities interact to
109 regulate ecosystem biomass production and its response to nutrient enrichment. For individual
110 plants, nutrient availability regulates biomass production by imposing physiological constraints
111 on growth (Droop 1974). Subsequently, guided by species niche and fitness differences and
112 species richness, interactions among individuals and species determine how the effects of

113 nutrients on individual growth add up to community level biomass production (Mellinger &
114 McNaughton 1975; Bakelaar & Odum 1978; Loreau 2010; Carroll *et al.* 2011). Resource limitation
115 influences this dynamic by providing opportunities for niche differences between species to
116 contribute to species coexistence (Levin 1970; Chesson 2000; Harpole & Tilman 2006). As such,
117 multiple nutrient enrichment can reduce species richness by constraining niche dimensionality
118 (Harpole & Tilman 2007; Harpole *et al.* 2016, 2017) and causing the competitive exclusion of
119 species that are less competitive in the new resource environment (Braakhekke & Hooftman
120 1999; Danger *et al.* 2008). This dynamic drives changes in community biomass production that
121 depend on the number and identity of enriching nutrients (Harpole *et al.* 2011; Fay *et al.* 2015).

122 The temporal variability of community biomass is driven by processes that control species
123 responses to environmental fluctuations (Tilman 1996; Loreau 2010). Declines in species richness
124 generally reduce the stability of biomass production (Hautier *et al.* 2015) by increasing the chance
125 of losing those species that can maintain function in a given environmental context (Loreau
126 2010). For example, temporal instability is frequently exacerbated when species that tolerate
127 extreme conditions such as drought or fire are lost (MacDougall *et al.* 2013). Community stability
128 is also influenced by changes in species synchrony, which regulate how species-level variability
129 scales to community-level variability to produce functional compensation (Hector *et al.* 2010;
130 Hautier *et al.* 2014; Gilbert *et al.* 2020; Valencia *et al.* 2020a). Synchrony measures the covariance
131 of species' responses to a fluctuating environment and is driven by niche differences and life-
132 history processes that impact the capacity for response (Loreau 2010). Together, these processes
133 guide fluctuations in species competitive rankings and result in compensatory dynamics, where
134 a functional decline by one species reduces competitive suppression of others, allowing them to

135 increase their biomass production (Brown *et al.* 2016). Consequently, nutrient enrichment and
136 multiple-nutrient interactions can influence the temporal variability of community biomass
137 production by influencing the number of niche differences that maintain species diversity and
138 guide species synchrony.

139 As the mean and temporal variability of biomass production may often be driven by these
140 mechanisms of species complementarity and species synchrony, respectively, there is the
141 potential for them to show different magnitudes of response to nutrient enrichment (Ives *et al.*
142 2000; Cardinale *et al.* 2013; Kohli *et al.* 2019). Transitions in the relationship between the mean
143 and variability of biomass production over time define changes in S and are an important
144 component of ecological stability (Ives & Carpenter 2007; Donohue *et al.* 2013). Declines in S
145 indicate increases in proportional variability and correspond to less consistent ecosystem
146 function (Donohue *et al.* 2016) and an increased likelihood of crossing minimum or maximum
147 thresholds (Carnus *et al.* 2014) where irreversible change in community composition or
148 functioning can occur (Beisner *et al.* 2003; Carpenter & Brock 2006). This transpires in enriched
149 systems if, despite higher average rates of production, concurrent increases in temporal
150 fluctuations enhance the risk that biomass production falls below a critical threshold (Scheffer *et*
151 *al.* 2001; Beisner *et al.* 2003; Carnus *et al.* 2014). While this paradox of enrichment dynamic is
152 well described in the theoretical literature (Rosenzweig 1971), its interaction with co-limitation
153 in empirical systems remains poorly characterized.

154 Here, we assessed the effects of individual and combined N, P and Potassium + essential
155 nutrients (K+) enrichment of 34 grassland sites spanning six continents over seven years. We
156 hypothesized that the effect of chronic nutrient enrichment on the temporal stability of biomass

157 production depends on nutrient identity and multiple-nutrient interactions and is partly driven
158 by factors including underlying co-limitation, local precipitation, species loss, and species
159 synchrony. We evaluated our hypotheses in three stages. First, we assessed temporal stability
160 under each treatment to determine if different individual and combined nutrient inputs had
161 different stability effects. Second, we assessed the mean and variability of biomass production
162 under each treatment to determine if changes in stability were mean- or variability-driven
163 (Carnus *et al.* 2014; Kohli *et al.* 2019). We expected to frequently observe variability-driven
164 destabilization because the mechanisms that control variability have shown strong responses to
165 enrichment (Hautier *et al.* 2014; Gilbert *et al.* 2020). Alternatively, synergistic responses to
166 multiple nutrient inputs could cause large increases in mean biomass that would mitigate against
167 destabilization (Harpole *et al.* 2011; Kaspari & Powers 2016). Finally, we assessed site differences
168 in stability responses and tested three potential mechanisms of different destabilization effects
169 among sites. First, we examined whether destabilization would be stronger where nutrient
170 limitation was stronger. Consequently, we expected N and P additions would have larger
171 destabilization effects than K⁺ because they are more commonly limiting (LeBauer & Treseder
172 2008; Fay *et al.* 2015; Hou *et al.* 2020). Similarly, we expected multiple nutrient enrichment would
173 cause greater destabilization than single nutrient inputs given frequent co-limitation (Harpole *et*
174 *al.* 2011; Fay *et al.* 2015). Second, we examined whether enrichment of sites with lower average
175 annual precipitation would have less effect on temporal variability because biomass is likely to
176 be more limited by water availability than nutrients (Paruelo *et al.* 1999; Huxman *et al.* 2004;
177 Morgan *et al.* 2016). Finally, we tested if changes in stability are driven by changes in species
178 richness (Hautier *et al.* 2015) or species synchrony (Loreau 2010; Valencia *et al.* 2020a), such that

179 stability decreases where species are lost or synchrony increases. We predicted that multiple
180 nutrient treatments would be more destabilizing than single nutrient treatments because they
181 are likely to cause greater species loss (Harpole & Tilman 2007; Harpole *et al.* 2016) and impose
182 greater constraints on the niche differences that permit asynchrony.

183

184 **METHODS**

185 **Experimental design and nutrient additions**

186 We assessed the mean, interannual variability and stability of aboveground biomass production
187 in 34 grassland sites that received standardized annual inputs of N, P and K⁺ for 7 years (Table
188 S1). These data are from the globally distributed Nutrient Network (NutNet) experiment,
189 described in Borer *et al.* (2014). Our decision to study a seven-year treatment period was made
190 to balance duration, thereby allowing temporal dynamics to unfold, with replication of sites,
191 thereby analyzing a broad range of grassland ecosystems. We tested the sensitivity of our
192 analyses to all subsets between one-three and one-twelve years (Table S2).

193 The majority of sites contain 3 blocks (but ranges from 1 to 6; Table S1) comprising 5 x 5
194 m treatment plots that receive one of the seven possible factorial combinations of N, P and K⁺
195 fertilizer, in addition to an unfertilized control plot. Plots are arranged in a randomized block
196 design. Nutrients were applied at a standardized yearly rate, using 10 g N (time-release urea) m⁻²
197 yr⁻¹, 10 g P (triple-super phosphate, which also includes Ca) m⁻² yr⁻¹, and 10 g K (potassium
198 sulphate, which also includes S) m⁻² yr⁻¹. In the first year only, all K plots also received 100 g m⁻²
199 of a macro- and micronutrient mix, comprising: 15% Fe, 14% S, 1.5% Mg, 2.5% Mn, 1% Cu, 1% Zn,
200 0.2% B, and 0.05% Mo – forming the K⁺ treatment. All plots included in this analysis were open

201 to herbivory. Site-level mean annual precipitation (MAP) and MAP variability data were obtained
202 from the WorldClim Global Climate database (Version 1.4; Hijmans *et al.* 2005).

203

204 **Metrics**

205 We harvested aboveground biomass annually from two 1 m x 10 cm strips in each plot at the site-
206 specific time of peak biomass production. Live biomass was separated from dead biomass, dried
207 at 60°C and weighed to provide estimated biomass production in $\text{g m}^{-2} \text{ year}^{-1}$ for each plot (Borer
208 *et al.* 2014). Harvest strips were relocated within a plot each year to avoid a clipping effect. We
209 calculated the temporal mean (μ) of biomass for each plot as the mean of annual biomass
210 measurements.

211 Ecosystems responding to chronic nutrient inputs can display directional trends in
212 biomass (Seabloom *et al.* 2021) that may influence stability metrics (Tilman *et al.* 2006; Lepš *et*
213 *al.* 2019). To focus our analysis on interannual fluctuations in biomass production, we detrended
214 our data by taking the residuals from a linear regression of biomass over years of treatment in
215 each plot (Tilman *et al.* 2006). Subsequently, the standard deviation of residuals in a plot (σ_{detr})
216 was used as a measure of interannual variability and in calculating a single detrended S value for
217 each plot, as: $S_d = \mu / \sigma_{detr}$. Values of S_d are presented as percentages in figures to indicate
218 proportional interannual variability (relative to treatment plot μ).

219 Plant species richness and percent cover to 1% were surveyed in permanent 1 m²
220 quadrats in each plot, based on visual assessment. Surveys were conducted annually or
221 biannually according to the growing season period at each site. We used these data to calculate
222 the temporal mean of species richness for each plot. Additionally, we used data for species'

223 percent cover to calculate detrended measures of temporal species synchrony in each plot, using
224 the `calc_sync` function (Lepš *et al.* 2019) in R (v 3.6.3; R Foundation for Statistical Computing).
225 This function detrends the ϕ synchrony metric (Loreau & de Mazancourt 2008) by aggregating ϕ
226 values from a moving 3-year window (ϕ_{t3} ; Lepš *et al.* 2019). This mitigates the influence of
227 directional trends, which can cause correlations in species abundances over time that are
228 separate from the year-to-year fluctuations that drive synchrony (Lepš *et al.* 2019; Valencia *et al.*
229 2020b). Values of ϕ_{t3} are bounded between 0 and 1, where 0 indicates perfect asynchrony and 1
230 indicates perfect synchrony.

231 We calculated treatment effects on each of these metrics using natural-log response
232 ratios, as: $LRR = \ln(treatment/control)$. This effect size highlights the change in the value of
233 a metric in a treatment plot relative to its value in a control plot located within the same
234 experimental block. It standardizes treatment effects across sites with different initial rates of
235 biomass production or variability. In addition, using LRRs centered values around zero and helped
236 data meet the conditions of normality that were assumed for our analysis (Hedges *et al.* 1999).
237 We back-transformed LRR estimates and converted them to % change relative to the control
238 treatment for presentation in figures.

239

240 **Analysis**

241 We used linear mixed effects models to test how different nutrient inputs impacted the S_d , μ ,
242 and σ_{detr} of grassland biomass. We assessed each metric using the model:

$$243 \quad LRR_{ijk} = \beta_i + b_j + \varepsilon_{ijk} \quad [1]$$

244 These models provide estimates for the fixed effect at each of the 7 levels of nutrient treatment
245 (i), estimates of random between-site variation in the response (j), and estimates of the within-
246 site variation (ijk) that results from observation of multiple blocks at each site. We chose this
247 model structure after trialing more complicated models including random slopes for the effect
248 of treatment within each, but these models did not converge. We also used model 1 to test for
249 nutrient effects on the LRRs of species richness and species synchrony. For each response, we
250 tested interactions between nutrients by replacing the nutrient term in model 1 with all two- and
251 three-way interactions between dummy coded N, P and K+ factors.

252 We assessed the dependence of stability responses on mean biomass responses using the
253 model:

$$254 \quad LRR.S_{d,ijk} = \beta_{1,i} + b_j + \beta_{2,i}\chi_i + \varepsilon_{ijk} \quad [2]$$

255 Where χ_i is the response of biomass in treatment i at site j . We built these models and obtained
256 estimates of model parameters by maximum likelihood estimation using the lme4 package (Bates
257 *et al.* 2015) in R.

258 We used a combination of methods to evaluate both the statistical and biological
259 significance of our effect size estimates (Nakagawa & Cuthill 2007). To assess statistical
260 significance, we present mean effects with their associated 95% confidence intervals and provide
261 P-values that indicate whether a treatment effect was significantly different from zero (at alpha
262 < 0.05). To interpret biological significance, we compare our results with effect sizes observed in
263 previous studies of grassland biomass production. For example, we used stability effects
264 observed in a meta-analysis of experimental biodiversity studies (Hautier *et al.* 2015) as a
265 benchmark for interpreting nutrient effects on stability in our analysis (Table S3). We used this

266 approach to determine the number of sites with predicted stability, mean biomass, and standard
267 deviation responses that passed thresholds of biological significance.

268 To test for potential drivers of among-site variation in nutrient treatment effects, we built
269 a second model for each of the three biomass responses. Fixed effect predictors included main
270 effects for plot-level LRRs of plant species richness and species synchrony, site-level MAP and
271 MAP variability, nutrient treatment, and the interaction effect of nutrient treatment with each
272 additional predictor. We evaluated the contribution of these factors to changes in the mean,
273 variability and stability of biomass production using a model selection approach. We used the
274 dredge function in the MuMIn package (Bartoń 2009) to determine which set of predictors and
275 interactions best explained the responses. We selected all predictors included in models within
276 four AIC of the most parsimonious model and obtained their full averages and associated
277 summary statistics using the model.avg function (Bartoń 2009).

278

279 **RESULTS**

280 **Do nutrient identity and nutrient interactions impact the temporal stability of grassland** 281 **biomass production?**

282 At the global scale, seven years of single nutrient N enrichment decreased S_d by 14% relative to
283 control plots ($LRR_N = -0.16$ $P < 0.001$; Fig. 1a, Table S4). Inputs of P were also generally
284 destabilizing ($LRR_P = -0.12$, $P = 0.011$). In contrast, K+ did not significantly affect S_d ($LRR_{K+} = -0.04$,
285 $P = 0.322$).

286 Multiple nutrient input treatments destabilized biomass (Fig. 1a, Table S4) by 13% with
287 NP ($LRR_{NP} = -0.14$, $P = 0.003$), 15% with NK+ ($LRR_{NK+} = -0.17$, $P < 0.001$), and 12% with NPK+

288 ($LRR_{NPK+} = -0.13, P = 0.004$). However, we did not observe destabilizing interactions between any
289 nutrients (Table S5). Instead, stability in NP, NK+ and NPK+ plots was equivalent to the stability
290 of single-nutrient N and P input plots. Further, sub-additive interactions between N and P acted
291 to stabilize biomass relative to the potential additive effect of N and P inputs ($LRR_{N*P} = 0.14, P =$
292 0.045).

293

294 **Do nutrient identity and nutrient interactions impact the temporal mean and variability of** 295 **grassland biomass production?**

296 At the global scale, increases in mean biomass following nutrient inputs were outpaced by
297 greater increases in temporal variability (Fig. 1b-c), a trend that defines decreases in S_d . Inputs
298 of N increased mean biomass production by 21% ($LRR_N = 0.19, P < 0.001$), while P ($LRR_P = 0.06, P$
299 $= 0.149$) and K+ ($LRR_{K+} = -0.001, P = 0.926$) did not significantly impact mean biomass globally
300 (Fig. 1b, Table S6). Concurrently, N additions increased the interannual variability of biomass by
301 40% ($LRR_N = 0.36, P < 0.001$) and P additions by 19% ($LRR_P = 0.17, P = 0.007$; Fig. 1c, Table S7). K+
302 inputs had no significant effect on σ_{detr} ($LRR_{K+} = 0.04, P = 0.5$).

303 Multiple nutrient addition effects on the mean and variability of biomass production were
304 larger than single nutrient effects. Inputs of NP, NK+, and PK+ increased mean biomass by 48%
305 ($LRR_{NP} = 0.39, P < 0.001$), 28% ($LRR_{NK+} = 0.26, P < 0.001$) and 16% ($LRR_{PK+} = 0.15, P < 0.001$),
306 respectively (Fig. 1b, Table S6). Concurrently, they increased interannual variability by 68% (LRR_{NP}
307 $= 0.52, P < 0.001$), 49% ($LRR_{NK+} = 0.42, P < 0.001$) and 21% ($LRR_{PK+} = 0.2, P = 0.002$), respectively
308 (Fig. 1c, Table S7). Simultaneous NPK+ additions increased mean biomass by 51% ($LRR_{NPK+} = 0.41,$

309 $P < 0.001$), exceeding the effect of all one- or two-nutrient treatments. Concurrently, NPK+
310 increased interannual variability by 68% ($LRR_{NPK+} = 0.53$, $P < 0.001$).

311 We observed a general synergistic co-limitation of mean biomass production by N and P
312 ($LRR_{N*P} = 0.14$, $P = 0.011$, Table S5). There was also a notable interaction between P and K+
313 ($LRR_{P*K+} = 0.1$, $P = 0.071$) that increased biomass in PK+ plots relative to controls. In contrast, we
314 did not observe any significant nutrient interactions for temporal variability (Table S5). Instead,
315 multiple nutrient effects on interannual variability were driven by significant effects of N and P
316 that produced additive increases in σ_{detr} (Table S5).

317

318 **How consistent were effects among the 34 globally distributed grassland sites?**

319 Destabilization most frequently occurred in response to treatments containing N. Inputs of N
320 alone decreased stability by more than 10% relative to control plots at 23 sites and by more than
321 20% at 8 sites (Table S8). These eight sites were globally distributed and did not follow a
322 detectable geographical trend. Similarly, large biomass and variability responses were most
323 frequently observed in response to N treatments. Mean biomass increased by over 25% with
324 NPK+ at 31 sites and by over 50% at 18 sites (Table S8). Variability increased by over 25% at 33
325 sites and by over 50% at 26 sites. Multiple nutrient treatments produced mean biomass and
326 variability responses more frequently than inputs of single nutrients (Table S8).

327

328 **Does nutrient limitation status impact the destabilization potential of nutrient enrichment?**

329 Across the study, sites with larger biomass responses, indicative of stronger underlying nutrient
330 limitations, were associated with larger destabilization responses to nutrient enrichment (Fig. 2,
331 Table S9). This relationship held for all nutrient combinations except NP and NPK+ (Table S9).

332

333 **Does average site precipitation influence the response of temporal stability to nutrient**
334 **enrichment?**

335 Average site precipitation did not strongly drive stability effects; MAP and MAP variability were
336 retained in the model selection procedure for the stability, mean biomass, and temporal
337 variability models but were not significant predictors of these responses (Table S10).

338

339 **Do nutrient effects on species richness or species synchrony influence the response of temporal**
340 **stability to nutrient enrichment?**

341 Species richness declined with N and all multiple nutrient treatments but was not generally
342 impacted by P or K+ alone (Fig. 3a, Table S11). Species loss was highest with simultaneous NPK+
343 inputs, which reduced species richness by 16% ($LRR_{NPK+} = -0.17$, $P < 0.001$) across the study.
344 Species synchrony did not display a clear directional response to any nutrient treatment at the
345 global scale (Fig. 3b, Table S12).

346 S_d was positively associated with changes in species richness ($P = 0.009$; Fig. 4a, Table S10).

347 Specifically, species loss was associated with decreased stability of biomass production whilst
348 species gains were associated with increased stability. In contrast, overall mean biomass
349 responses were negatively associated with species richness such that biomass was most likely to
350 increase where species were lost ($P = 0.001$; Fig. 4b, Table S10). Similarly, change in the

351 interannual variability of biomass production was negatively associated with species richness
352 such that plots displayed greater increases in temporal variability where species loss was higher
353 ($P < 0.001$; Fig. 4c, Table S10).

354 There was a negative relationship between species synchrony and S_d responses ($P = 0.052$;
355 Fig. 5, Table S10). Consequently, destabilization of community biomass was more likely where
356 nutrients caused species synchrony to increase, and stabilization more likely where nutrients
357 promoted asynchrony (Fig. 5). Species synchrony was retained in the model set for the mean and
358 variability of biomass but was not a statistically significant predictor of these responses (Table
359 S10).

360

361 **DISCUSSION**

362 **Do nutrient identity and nutrient interactions impact the temporal stability, mean and** 363 **variability of grassland biomass production?**

364 Grassland biomass production is often limited or co-limited by nutrients (Harpole et al. 2011; Fay
365 et al. 2015). However, understanding of how co-limitation dynamics affect grassland stability is
366 still lacking. This is crucial to assessing the reliability of critical ecosystem services or threat of
367 eventual ecological collapse in nutrient enriched environments (McCann et al. 2020). Our
368 analyses showed that N and multiple nutrient enrichment generally increased mean biomass
369 production but destabilized it by inducing even greater increases in temporal variability. This
370 signals some years of elevated biomass production but also that the magnitude of fluctuations
371 between years increased with N supply. Enrichment of P did not generally increase mean biomass
372 but still increased its temporal variability and therefore had a general destabilizing effect. In

373 contrast, K⁺ enrichment did not change either the mean or variability of biomass, and therefore
374 did not impact stability at the global scale.

375 Multiple nutrient treatments revealed interactive effects on mean biomass production,
376 including a general synergistic interaction between N and P, consistent with previous
377 observations of co-limitation (Harpole *et al.* 2011; Fay *et al.* 2015; Kaspari *et al.* 2017). However,
378 this did not directly translate to stability responses. Multiple nutrient inputs did not drive
379 transitions in mean-variability scaling beyond the effects of single N or P inputs. Consequently,
380 nutrient interaction effects on stability were generally sub-additive (i.e. less than the sum of
381 multiple single-nutrient effects; Harpole *et al.* 2011). This mitigated against compounding
382 destabilization effects that could occur if all added nutrients exerted additive or synergistic
383 effects (Harpole *et al.* 2011).

384 Accordingly, we did not find evidence that multiple-nutrient enrichment was more
385 destabilizing than single-nutrient enrichment at the global scale. This suggests that nutrient input
386 identity and interactions can have consequences for trade-offs between increased grassland
387 biomass production and the risk of destabilization. That is, declining S_d may indicate an increased
388 risk of reaching thresholds corresponding to a minimum acceptable value of an ecosystem
389 function (Carnus *et al.* 2014) where, for example, substantial changes to community composition
390 become likely (Scheffer *et al.* 2001; Beisner *et al.* 2003; Carpenter & Brock 2006; McCann *et al.*
391 2021) or a food production system fails to reach a profit. Our study suggests that, relative to
392 control plots, single N inputs generally produced higher mean biomass production (more reward)
393 but decreased stability (more risk). In contrast, relative to N, multiple-nutrient NP and NPK⁺
394 inputs generally produced higher mean biomass but with an equivalent S_d .

395 All inputs containing N generally increased temporal fluctuations in biomass production,
396 consistent with previous empirical observation (Hautier *et al.* 2014) and theoretical work on the
397 paradox of enrichment (Rosenzweig 1971). However, while NP and NPK+ produced the same risk
398 as N-only inputs, they offered greater biomass production; potentially equating to greater
399 delivery of ecosystem services such as food production, food system profitability, biofuels and
400 soil carbon sequestration (Kremen 2005; Gounand *et al.* 2020). Nonetheless, situations where S_d
401 is equivalent but means are different indicate that total interannual variability is greater in the
402 high means group. Variability can be of interest itself as it determines the absolute size of
403 fluctuations in ecosystem services (Kohli *et al.* 2019). In this study, absolute variability was higher
404 in NP and NPK+ treatments than with N only, despite equivalent S_d values; a result that could
405 still translate to altered nutrient cycling or secondary production (Kohli *et al.* 2019). These
406 intricacies highlight the necessity of being clear about the aspects of variability and stability that
407 are of concern in a given context (Carnus *et al.* 2014; Kohli *et al.* 2019).

408 Here, explicit consideration of nutrient effects on both the mean and variability of
409 biomass indicated a general effect in which adding limiting nutrients increased mean biomass
410 production but drove disproportionate increases in variability, resulting in variability-driven
411 destabilization. It also revealed that the type of multiple nutrient limitation of the mean
412 (synergistic vs additive; Harpole *et al.* 2011) was not the same as multiple limitation of temporal
413 variability. While consideration of both the mean and variability components of stability remain
414 relatively uncommon (Carnus *et al.* 2014; Hautier *et al.* 2015; Kohli *et al.* 2019; Avolio *et al.* 2020),
415 global change drivers do not always appear to alter mean-variability proportionality. For
416 example, Kohli *et al.* (2019) observed that disturbance of consumer food webs had no effect on

417 the stability of grassland biomass production because the mean and variability responded
418 proportionately. These results show that future work should routinely consider how both the
419 mean and variability of ecosystem processes respond to key global changes (Avolio *et al.* 2020).

420

421 **How consistent was nutrient-driven destabilization among 34 globally distributed grassland**
422 **sites?**

423 The magnitude of nutrient-driven changes in stability varied among sites. Twenty sites displayed
424 10% declines in stability following NPK+ enrichment and eight displayed reductions in stability of
425 more than 20%. This effect size has a similar magnitude to previously reported stability
426 responses. For example, declining species richness is a widely acknowledged driver of significant
427 destabilization (Tilman *et al.* 2006; Isbell *et al.* 2013; Hautier *et al.* 2015) and, in a recent meta-
428 analysis, experimentally reducing richness from 16 to 2 was also shown to destabilize biomass
429 production by 20% (Hautier *et al.* 2015). This suggests that the effects of nutrient enrichment on
430 stability can match other key global change drivers. Overall, our study suggests that there is a
431 wide range in the magnitude of grassland stability responses to elevated nutrient supply, but that
432 increasing eutrophication will likely drive more grasslands towards critical thresholds of
433 functioning.

434 Nutrient effects on mean biomass production were more prevalent across all the sites. At
435 31 sites, NPK+ enrichment increased mean biomass production by at least 25%. Nutrient
436 limitation has not appeared this prevalent in previous, shorter assessments. For example,
437 previous analyses of NutNet data showed that over 3-5 years 12 of 42 sites were not significantly
438 limited by any combination of N, P and K+ (Fay *et al.* 2015). We included nine of those sites in the

439 present study and, after seven years, NPK+ had driven >30% increases in biomass production at
440 eight of them. This is consistent with increasing nutrient effects observed over ten years
441 (Seabloom *et al.* 2021) and might be explained by a progressive shift in community composition,
442 as opposed to immediate and possibly transient changes in relative abundance and individual
443 biomass production. Nutrient effects on temporal variability were even more prevalent, with 33
444 sites increasing variability by 25% and 26 sites increasing variability by 50% following NPK+
445 enrichment.

446

447 **Was there evidence for mechanisms associated with destabilization following nutrient**
448 **enrichment?**

449 Understanding of the mechanisms that determine the potential for different nutrients to
450 destabilize grassland production is crucial to mitigating the risk of destabilization in a given
451 environmental context. In our analysis, there was no clear association of nutrient-driven
452 destabilization with MAP or MAP variability. This contrasts our prediction that site precipitation
453 would mediate nutrient effects on biomass stability, based on foundational work suggesting the
454 effect of nutrient limitation on grassland biomass production decreases with increasing moisture
455 limitation (Paruelo *et al.* 1999; Huxman *et al.* 2004). However, our finding is consistent with
456 broader observations that nutrient enrichment can destabilize biomass production in both wet
457 (Tilman *et al.* 2006) and dry (Wang *et al.* 2017) grassland systems. One explanation for this
458 pattern is that different mechanisms mediate the relationship between moisture availability and
459 stability in wet and dry systems, but each still promote destabilization (Wang *et al.* 2017).
460 Nutrient enrichment of wet grasslands often reduces stability by reducing species richness and

461 negating positive diversity-stability effects (Tilman *et al.* 2006; Wang *et al.* 2017). In contrast, in
462 dry grasslands, nutrient enrichment may increase the responsiveness of biomass production to
463 occasional wet years, therefore generating larger temporal fluctuations through occasional
464 increases in growth and, ultimately, reducing stability (Wang *et al.* 2017). Studies that assess wet
465 and dry grasslands separately have provided better insight the role of precipitation and moisture
466 availability in mediating nutrient effects on the stability of grassland biomass production (Bharath
467 *et al.* 2020).

468 Our study suggests that destabilization following nutrient enrichment is partly driven by
469 the extent of underlying nutrient limitation, meeting our expectation that destabilization
470 responses would be stronger where nutrient limitation is stronger. One explanation for this is
471 that nutrient limitations may impose constraints on community composition by mediating
472 competition among species (Tilman 1982; Braakhekke & Hooftman 1999). Enrichment of strongly
473 nutrient-limited communities may cause shifts in the outcomes of competitive interactions
474 (Tilman 1982) and changes in community composition that impact community biomass
475 production. Despite the overall relationship mean and stability effects, the response of mean
476 biomass was not a significant predictor of stability within the NP and NPK+ treatments, suggesting
477 these inputs also reduced stability where they did not limit biomass production. One explanation
478 for this is that NP and NPK+ enrichment can drive species loss even where those nutrients are
479 not limiting factors (Harpole *et al.* 2016), thereby causing destabilization through lost diversity-
480 stability effects, as discussed below.

481 Our results also supported the prediction that nutrient effects on species richness would
482 contribute to changes in mean biomass production and its stability (Hautier *et al.* 2015). Plots

483 that lost more species typically became more productive but less stable due to proportionally
484 larger increases in the temporal standard deviation of biomass production. This has not been
485 observed in previous analyses of NutNet data (Hautier *et al.* 2014, 2020). Our current findings
486 better match theoretical predictions about diversity-stability relationships, and our ability to
487 detect this here is likely due to the increased power afforded by including observations from all
488 treatment plots (more than just NPK+ plots) and the accumulation of more sites with longer-term
489 data. In addition to species richness effects, we also found that changes in species synchrony
490 following enrichment contributed to changes in stability. Overall, stability was reduced where
491 synchrony increased, in agreement with previous work (Loreau & de Mazancourt 2008; Hautier
492 *et al.* 2014, 2020; Muraina *et al.* 2021). However, in contrast to richness, there were no general
493 effects of nutrient treatments on synchrony, nor differences between treatments.

494 In addition to decreased stability in response to nutrient enrichment observed here, our
495 results also suggest a heightened destabilization risk over longer periods of chronic enrichment.
496 Coupled with evidence that species loss can continue for more than a decade with simultaneous
497 NPK+ enrichment (Seabloom *et al.* 2021), our observation that species richness loss contributed
498 to nutrient-driven destabilization suggests that increased variability could be exacerbated over
499 longer periods. Further, our observation of increased overall mean biomass production with
500 species loss was characteristic of a shift in community composition towards highly productive
501 species (Tilman 1982; Harpole & Tilman 2007; Hautier *et al.* 2009). Productive species can
502 mitigate against destabilization by maintaining a high temporal mean; however, sites with higher
503 species loss may be more susceptible to future crashes in productivity driven by increased
504 sensitivity to other environmental variability such as drought, herbivory, or fire (MacDougall *et*

505 *al.* 2013). This would negate mean-driven stabilization effects and exacerbate destabilization.
506 This dynamic can lead to a collapse in biomass production over longer timeframes (Isbell *et al.*
507 2013). This long-term effect is more likely with increasing numbers of added nutrients, which can
508 cause increasing species loss (Harpole & Tilman 2007; Harpole *et al.* 2016). Our findings suggest
509 this risk is particularly enhanced with N and the NP interaction that drove the greatest species
510 loss.

511

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521

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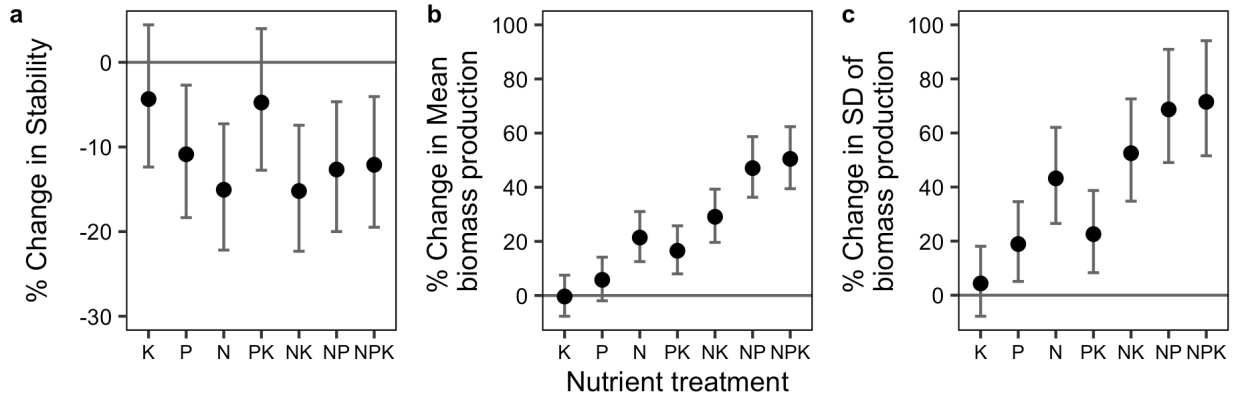
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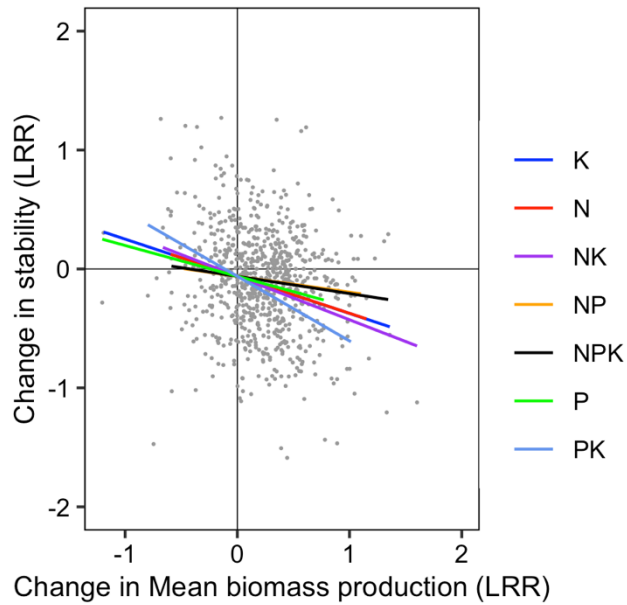
689 **FIGURES**



690
 691 **Figure 1.** Effect of seven years of single- and multiple-nutrient additions on the detrended
 692 stability **(a)**, temporal mean **(b)**, and detrended standard deviation (SD) **(c)** of grassland biomass
 693 production in 34 sites. Different individual and combined additions of nitrogen (N), phosphorus
 694 (P), and potassium with essential nutrients (K) influenced the magnitude of stability, mean and
 695 variability responses. The points show percent change relative to unenriched control plots. They
 696 represent back-transformed fixed effect estimates (with 95% confidence intervals) from mixed
 697 effects models that accounted for site as a random grouping factor. See Supplementary
 698 Information for detailed model specification and summary statistics.

699

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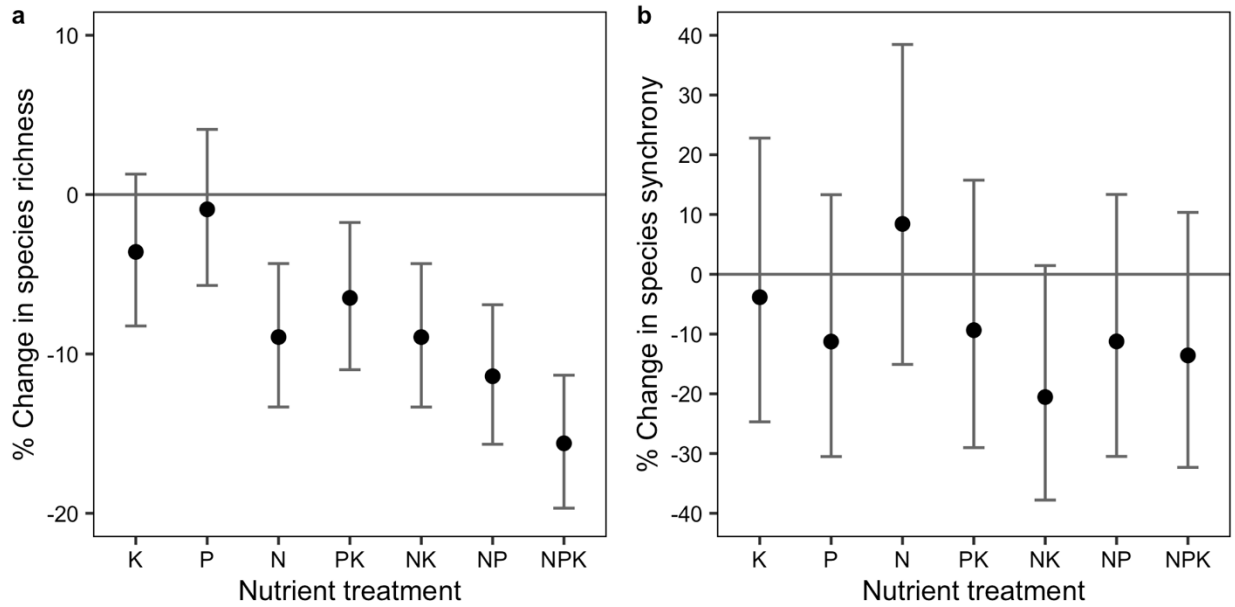
701

702 **Figure 2.** Relationship between change in mean biomass production and change in stability under
703 seven years of different individual and combined additions of nitrogen (N), phosphorus (P), and
704 potassium with essential nutrients (K). Larger biomass responses were associated with larger
705 declines in stability for all treatments except NP and NPK. Points show plots within blocks at 34
706 grassland sites. Colored lines are fixed-effect regression slopes for each treatment from mixed
707 effects models. See Supplementary Information for detailed model specification and summary
708 statistics.

709

710

711

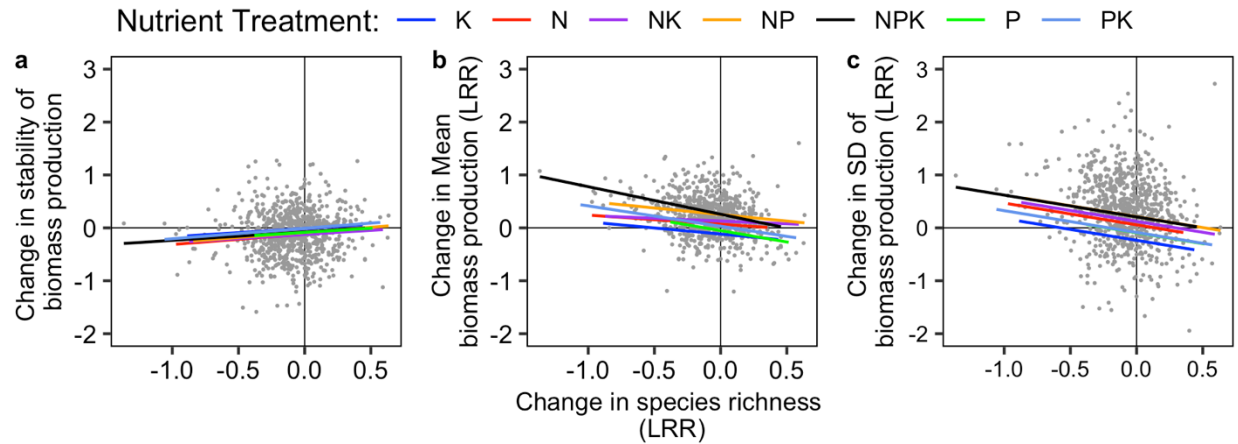


712

713 **Figure 3.** Effect of individual and combined additions of nitrogen (N), phosphorus (P), and
714 potassium with essential nutrients (K) on the temporal mean of species richness **(a)** and
715 detrended species synchrony **(b)** in 34 grassland sites. Points show fixed effect estimates with
716 95% confidence intervals (see Fig. 1 caption and Supplementary Information).

717

718



719

720 **Figure 4.** Nutrient-driven changes in species richness contribute to nutrient effects on the

721 temporal stability (a), mean (b), and standard deviation (SD) (c) of grassland biomass production.

722 Points show plots within blocks at 34 globally distributed grassland sites. Colored lines are fixed-

723 effect regression slopes from mixed effects models for individual and combined nitrogen (N),

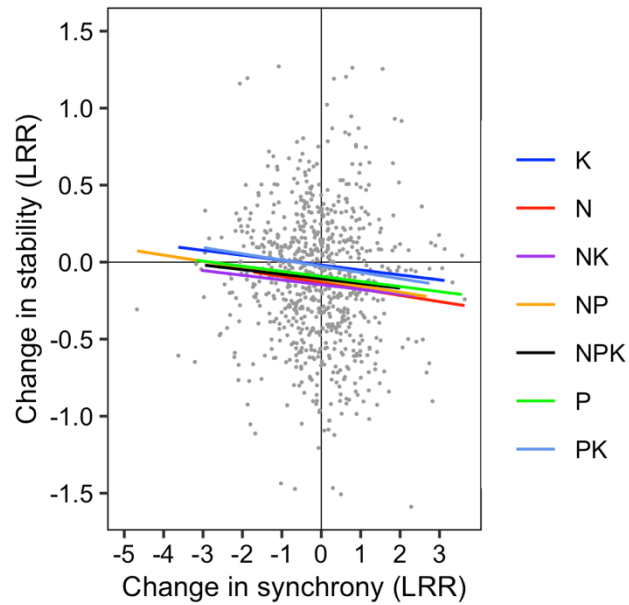
724 phosphorus (P), and potassium with essential nutrients (K) addition treatments. Similar trends

725 caused overlapping lines for some treatments in panels a (PK overlaps P) and c (PK overlaps K).

726 See Supplementary Information for detailed model specification and summary statistics.

727

728



729

730

731 **Figure 5.** Nutrient-driven changes in species synchrony contribute to nutrient effects on the
732 stability of grassland biomass production over seven years. Colored lines show fixed-effect slopes
733 within different nitrogen (N), phosphorus (P), and potassium with essential nutrients (K)
734 treatments (see Fig. 4 caption and Supplementary Information).

735 **SUPPLEMENTARY INFORMATION**

736 **Table S1.** Summary of site characteristics for the 34 sites included in the study. Sites were located
 737 in 9 countries across 6 continents. Sites typically had 3 experimental blocks, but this ranged from
 738 1-6. The sites span a broad gradient of site-level plant species richness, mean annual precipitation
 739 (MAP; mm), and mean annual temperature (MAT; °C). Data beyond seven years were removed
 740 where applicable. For sites with missing data, the available years of treatment data that were
 741 used in the analysis are indicated in the ‘years’ column.

Site	Country	Continent	Lat.	Long.	Elevation	Blocks	Richness	MAP	MAT	Years
bldr.us	US	N. America	40.0	-105.2	1633	2	49	487	9.9	1-7
bnch.us	US	N. America	44.3	-122.0	1318	3	61	1618	6.8	1-7
bogong.au	AU	Australia	-36.9	147.3	1760	3	51	1678	6	1-7
burrawan.au	AU	Australia	-27.7	151.1	425	3	45	643	18	1-7
cbgb.us	US	N. America	41.8	-93.4	275	6	113	871	9.3	1-7
cdcr.us	US	N. America	45.4	-93.2	270	5	142	740	6.3	1-7
cdpt.us	US	N. America	41.2	-101.6	965	6	85	456	9.6	1-7
comp.pt	PT	Europe	38.8	-8.8	200	3	105	564	17	1-7
cowi.ca	CA	N. America	48.8	-123.6	50	3	29	762	10	1-7
elliott.us	US	N. America	32.9	-117.1	200	3	51	344	18	1-7
frue.ch	CH	Europe	47.1	8.5	995	3	40	1546	7	1-7
hall.us	US	N. America	36.9	-86.7	194	3	53	1289	14	1-7
hopl.us	US	N. America	39.0	-123.1	598	3	132	1065	13	1-7
kibber.in	IN	Asia	32.3	78.0	4241	3	37	400	-1.5	1-4,6
kiny.au	AU	Australia	-36.2	143.8	90	3	114	408	16	1-7
koffler.ca	CA	N. America	44.0	-79.5	301	3	51	853	6.3	1-7
konz.us	US	N. America	39.1	-96.6	440	3	109	889	12	1-5,7
lancaster.uk	UK	Europe	54.0	-2.6	180	3	34	1522	8	1-3,6,7
look.us	US	N. America	44.2	-122.1	1500	3	62	1877	6.9	1-7
marc.ar	AR	S. America	-37.7	-57.4	6	3	67	907	14	1-7
mcla.us	US	N. America	38.9	-122.4	642	3	88	936	14	1-7
mtca.au	AU	Australia	-31.8	117.6	285	4	71	324	18	1-7
saline.us	US	N. America	39.0	-99.1	440	3	122	608	12	1-7
sedg.us	US	N. America	34.7	-120.0	550	3	34	478	16	1-7
sevi.us	US	N. America	34.4	-106.7	1600	1	85	252	13	1-7
sgs.us	US	N. America	40.8	-104.8	1650	3	78	369	8.9	1-7
shps.us	US	N. America	44.2	-112.2	910	4	97	246	5.3	1-5
sier.us	US	N. America	39.2	-121.3	197	5	128	936	16	1-7
smith.us	US	N. America	48.2	-122.6	62	3	66	605	10	1-5
spin.us	US	N. America	38.1	-84.5	271	3	52	1152	13	1-7
temple.us	US	N. America	31.0	-97.3	184	3	99	877	19	1-7
trel.us	US	N. America	40.1	-88.8	200	3	25	992	11	1-7
ukul.za	ZA	Africa	-29.7	30.4	842	3	176	832	18	1-7
valm.ch	CH	Europe	46.6	10.4	2320	3	122	681	0.1	1-7

743 **Table S2.** Assessment of the sensitivity of detrended stability effect size (LRRs) estimates from
744 model 1 to the number of years assessed. We analyzed data for seven treatment years. This
745 choice impacted the length of time available for temporal dynamics to unfold as well as the
746 number of sites it was possible to use in the analysis. Significant effect sizes at alpha 0.05 are
747 shown in bold and underlined. Effect sizes with P values below alpha 0.1 are underlined. The
748 effects presented in the paper were most representative of those seen in subsets of between 1-
749 6 and 1-9 years of treatment, which included from 43 to 28 sites, respectively.

Years	Sites	Parameter	Nutrient Treatment						
			K	P	N	PK	NK	NP	NPK
3	70	Estimate	0.028	0.059	0.001	0.096	0.076	0.077	-0.034
		<i>P</i>	0.642	0.335	0.986	0.115	0.212	0.208	0.573
4	58	Estimate	-0.010	-0.055	<u>-0.119</u>	0.019	-0.045	0.011	-0.078
		<i>P</i>	0.853	0.312	<u>0.030</u>	0.732	0.415	0.837	0.155
5	51	Estimate	-0.024	-0.059	<u>-0.083</u>	-0.017	-0.058	-0.003	-0.076
		<i>P</i>	0.625	0.238	<u>0.099</u>	0.741	0.245	0.956	0.128
6	43	Estimate	-0.028	<u>-0.078</u>	<u>-0.104</u>	-0.046	<u>-0.122</u>	-0.035	<u>-0.087</u>
		<i>P</i>	0.541	<u>0.093</u>	<u>0.025</u>	0.321	<u>0.009</u>	0.455	<u>0.061</u>
7	34	Estimate	-0.044	<u>-0.115</u>	<u>-0.163</u>	-0.049	<u>-0.165</u>	<u>-0.135</u>	<u>-0.129</u>
		<i>P</i>	0.322	<u>0.011</u>	<u><0.001</u>	0.278	<u><0.001</u>	<u>0.003</u>	<u>0.004</u>
8	29	Estimate	-0.026	<u>-0.092</u>	<u>-0.135</u>	-0.061	<u>-0.140</u>	<u>-0.109</u>	<u>-0.122</u>
		<i>P</i>	0.573	<u>0.051</u>	<u>0.004</u>	0.194	<u>0.003</u>	<u>0.021</u>	<u>0.010</u>
9	28	Estimate	-0.032	<u>-0.071</u>	<u>-0.122</u>	-0.048	<u>-0.114</u>	<u>-0.107</u>	<u>-0.119</u>
		<i>P</i>	0.444	<u>0.090</u>	<u>0.004</u>	0.255	<u>0.007</u>	<u>0.011</u>	<u>0.005</u>
10	21	Estimate	-0.001	-0.034	-0.035	0.006	<u>-0.090</u>	-0.030	-0.017
		<i>P</i>	0.979	0.484	0.472	0.908	<u>0.064</u>	0.531	0.722
11	16	Estimate	0.030	-0.037	-0.050	0.004	<u>-0.113</u>	-0.053	-0.069
		<i>P</i>	0.547	0.463	0.325	0.934	<u>0.027</u>	0.296	0.175
12	6	Estimate	-0.025	-0.007	-0.070	-0.036	-0.087	-0.052	<u>-0.114</u>
		<i>P</i>	0.685	0.915	0.258	0.561	0.158	0.399	<u>0.066</u>

750

751

752 **Table S3.** Effect sizes of the temporal mean, standard deviation and stability of grassland biomass
 753 production in response to well-established mechanisms of function and stability. We present this
 754 range of log response ratios (LRR) to aid interpretation of the biological significance of our results.
 755 Here, the effect sizes denote the impact of the listed experimental manipulation relative to
 756 control conditions within the study. The references used to provide these benchmarks include
 757 meta-analysis of multiple studies of stability effects (1), as well as assessment of sites with a wide
 758 geographical distribution (2).

Response	LRR	% change	Examples from previous grassland studies	Ref*
Biomass	0.22	25	LRR = 0.24: N enrichment - 34 kg ha ⁻¹ / 3.4 g m ²	(1)
			LRR = 0.27: Benchmark for biologically significant mean biomass response	(2)
	0.4	50	LRR = 0.57: N enrichment - 54 kg ha ⁻¹ / 5.4 g m ²	(3)
	0.56	75	LRR = 0.66: N enrichment - 270 kg ha ⁻¹ / 27 g m ²	(1)
		LRR = 0.74: Increasing species richness from 1 to 16	(2)	
SD	0.22	25	LRR = 0.24: Reducing species richness from 16 to 4	(1)
	0.4	50	LRR = 0.48: N enrichment - 54 kg ha ⁻¹ / 5.4 g m ²	(1)
			LRR = 0.48: Reducing species richness from 16 to 2	
	0.56	75	LRR = 0.60: Reducing species richness from 16 to 1	(1)
<i>S_d</i>	-0.11	-10	LRR = -0.11: N enrichment - 54 kg ha ⁻¹ / 5.4 g m ²	(1)
	-0.22	-20	LRR = 0.22: Reducing species richness from 16 to 2	(1)
			LRR = 0.29: N enrichment - 270 kg ha ⁻¹ / 27 g m ²	(1)
	-0.43	-35	LRR = 0.41: Reducing species richness from 16 to 1	(1)

* (1): Hautier et al., 2015; (2): Fay et al., 2015; (3): Tilman et al., 2012

759

760



761 **Table S4. Model summary for nutrient treatment effects on stability**

762
 763 Linear mixed model fit by REML. t-tests use Satterthwaite's method
 764 ['lmerModLmerTest']
 765 Formula: lrr.detr.s ~ 0 + trt + (1 | site_code)
 766 Data: lrr
 767
 768 REML criterion at convergence: 886.6
 769
 770 Scaled residuals:
 771 Min 1Q Median 3Q Max
 772 -3.7009 -0.6123 0.0431 0.5866 3.2800
 773
 774 Random effects:
 775 Groups Name Variance Std.Dev.
 776 site_code (Intercept) 0.01586 0.1259
 777 Residual 0.16906 0.4112
 778 Number of obs: 777, groups: site_code, 34
 779
 780 Fixed effects:
 781 Estimate Std. Error df t value Pr(>|t|)
 782 trtK -0.04438 0.04474 232.60035 -0.992 0.322231
 783 trtN -0.16315 0.04474 232.60035 -3.647 0.000328 ***
 784 trtNK -0.16495 0.04474 232.60035 -3.687 0.000283 ***
 785 trtNP -0.13540 0.04474 232.60035 -3.026 0.002753 **
 786 trtNPK -0.12904 0.04474 232.60035 -2.884 0.004291 **
 787 trtP -0.11504 0.04474 232.60035 -2.571 0.010752 *
 788 trtPK -0.04869 0.04474 232.60035 -1.088 0.277538
 789 ---
 790 Signif. codes: 0 '***', 0.001 '**', 0.01 '*', 0.05 '.', 0.1
 791 ' ', 1
 792
 793 Correlation of Fixed Effects:
 794 trtK trtN trtNK trtNP trtNPK trtP
 795 trtN 0.239
 796 trtNK 0.239 0.239
 797 trtNP 0.239 0.239 0.239
 798 trtNPK 0.239 0.239 0.239 0.239
 799 trtP 0.239 0.239 0.239 0.239 0.239
 800 trtPK 0.239 0.239 0.239 0.239 0.239 0.239
 801

802 **Table S5. Tests of nutrient interactions**

803

804 **Stability of biomass:**

805

806 lrr.detr.s ~ 0 + N * P * K + (1 | site_code)

807

Nutrient	Estimate	SE	df	t.value	P
N	-0.163	0.045	232.600	-3.647	0.000
P	-0.115	0.045	232.600	-2.571	0.011
K	-0.044	0.045	232.600	-0.992	0.322
N:P	0.143	0.071	628.152	2.010	0.045
N:K	0.043	0.071	628.152	0.599	0.549
P:K	0.111	0.071	628.152	1.558	0.120
N:P:K	-0.103	0.106	762.413	-0.972	0.331

816

817

818 **Mean biomass:**

819

820 lrr.mean ~ 0 + N * P * K + (1 | site_code)

821

Nutrient	Estimate	SE	df	t.value	P
N	0.194	0.039	111.782	5.003	0.000
P	0.056	0.039	111.782	1.453	0.149
K	-0.004	0.039	111.782	-0.094	0.926
N:P	0.135	0.056	361.270	2.421	0.016
N:K	0.065	0.056	361.270	1.161	0.246
P:K	0.100	0.056	361.270	1.796	0.073
N:P:K	-0.139	0.080	655.989	-1.740	0.082

830

831

832 **SD of biomass:**

833

834 lrr.detr.sd ~ 0 + N * P * K + (1 | site_code)

835

Nutrient	Estimate	SE	df	t.value	P
N	0.359	0.063	198.778	5.688	0.000
P	0.173	0.063	198.778	2.745	0.007
K	0.043	0.063	198.778	0.675	0.500
N:P	-0.009	0.098	577.917	-0.096	0.924
N:K	0.020	0.098	577.917	0.207	0.836
P:K	-0.012	0.098	577.917	-0.125	0.901
N:P:K	-0.034	0.145	752.494	-0.235	0.814

844

845 **Table S6. Model summary for nutrient treatment effects on mean biomass production**

846
847 Linear mixed model fit by REML. t-tests use Satterthwaite's method [
848 lmerModLmerTest]
849 Formula: lrr.mean ~ 0 + trt + (1 | site_code)
850 Data: lrr
851
852 REML criterion at convergence: 423.3
853
854 Scaled residuals:
855 Min 1Q Median 3Q Max
856 -3.1935 -0.6635 0.0369 0.5792 5.4567
857
858 Random effects:
859 Groups Name Variance Std.Dev.
860 site_code (Intercept) 0.02348 0.1532
861 Residual 0.08955 0.2992
862 Number of obs: 777, groups: site_code, 34
863
864 Fixed effects:
865 Estimate Std. Error df t value Pr(>|t|)
866 trtK -0.003631 0.038804 111.782393 -0.094 0.92561
867 trtN 0.194117 0.038804 111.782393 5.003 0.00000211930 ***
868 trtNK 0.255324 0.038804 111.782393 6.580 0.00000000158 ***
869 trtNP 0.385740 0.038804 111.782393 9.941 < 0.00000000000000002 ***
870 trtNPK 0.408658 0.038804 111.782393 10.531 < 0.00000000000000002 ***
871 trtP 0.056391 0.038804 111.782393 1.453 0.14896
872 trtPK 0.153058 0.038804 111.782393 3.944 0.00014 ***
873 ---
874 Signif. codes: 0 '***', 0.001 '**', 0.01 '*', 0.05 '.', 0.1
875 ', 1
876
877 Correlation of Fixed Effects:
878 trtK trtN trtNK trtNP trtNPK trtP
879 trtN 0.464
880 trtNK 0.464 0.464
881 trtNP 0.464 0.464 0.464
882 trtNPK 0.464 0.464 0.464 0.464
883 trtP 0.464 0.464 0.464 0.464 0.464
884 trtPK 0.464 0.464 0.464 0.464 0.464 0.464
885
886

887 **Table S7. Model summary for nutrient treatment effects on biomass temporal variability**

888
889 Linear mixed model fit by REML. t-tests use Satterthwaite's method [
890 lmerModLmerTest]
891 Formula: lrr.detr.sd ~ 0 + trt + (1 | site_code)
892 Data: lrr
893
894 REML criterion at convergence: 1372.5
895
896 Scaled residuals:
897 Min 1Q Median 3Q Max
898 -3.2911 -0.6016 -0.0416 0.6161 4.2848
899
900 Random effects:
901 Groups Name Variance Std.Dev.
902 site_code (Intercept) 0.03809 0.1952
903 Residual 0.31538 0.5616
904 Number of obs: 777, groups: site_code, 34
905
906 Fixed effects:
907 Estimate Std. Error df t value Pr(>|t|)
908 trtK 0.04262 0.06313 198.77816 0.675 0.50042
909 trtN 0.35914 0.06313 198.77816 5.688 0.00000004537297638 ***
910 trtNK 0.42214 0.06313 198.77816 6.686 0.00000000022616030 ***
911 trtNP 0.52301 0.06313 198.77816 8.284 0.00000000000001739 ***
912 trtNPK 0.53957 0.06313 198.77816 8.546 0.000000000000000334 ***
913 trtP 0.17330 0.06313 198.77816 2.745 0.00661 **
914 trtPK 0.20362 0.06313 198.77816 3.225 0.00147 **
915 ---
916 Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1
917 ' ' 1
918
919 Correlation of Fixed Effects:
920 trtK trtN trtNK trtNP trtNPK trtP
921 trtN 0.287
922 trtNK 0.287 0.287
923 trtNP 0.287 0.287 0.287
924 trtNPK 0.287 0.287 0.287 0.287
925 trtP 0.287 0.287 0.287 0.287 0.287
926 trtPK 0.287 0.287 0.287 0.287 0.287 0.287
927

928 **Table S8.** Number of grassland sites (total = 34) at which predicted biomass and stability
 929 responses to nutrient inputs exceeded effects demonstrated elsewhere in the literature. See the
 930 text and Table S2 for a description of comparable effect sizes.

	Mean biomass			Standard dev. (σ_{resid})			CV_{detr}^{-1}		
	0.22	0.4	0.56	0.22	0.4	0.56	-0.11	-0.22	-0.43
LRR:	25	50	75	25	50	75	-10	-20	-35
% Change:									
K	1	0	0	5	0	0	8	0	0
P	4	0	0	12	3	0	19	7	0
N	13	1	0	25	12	3	23	8	0
PK	9	1	0	13	3	0	8	0	0
NK	21	4	1	28	16	7	24	8	0
NP	30	15	4	33	25	13	21	8	0
NPK	31	18	5	33	26	15	20	8	0

931

932 **Table S9.** Model summary for relationship between mean biomass response and stability

933 response:

934

935 Linear mixed model fit by maximum likelihood . t-tests use Satterthwaite's
936 method ['lmerModLmerTest']

937 Formula: lrr.detr.s ~ trt:lrr.mean + (1 | site_code)

938 Data: lrr

939

AIC	BIC	logLik	deviance	df.resid
829.9	876.5	-405.0	809.9	767

942

943 Scaled residuals:

Min	1Q	Median	3Q	Max
-3.5586	-0.6277	0.0145	0.6153	3.5164

946

947 Random effects:

Groups	Name	Variance	Std.Dev.
site_code	(Intercept)	0.01723	0.1313
	Residual	0.15732	0.3966

951 Number of obs: 777, groups: site_code, 34

952

953 Fixed effects:

	Estimate	Std. Error	df	t value	Pr(> t)
(Intercept)	-0.06156	0.02849	41.51052	-2.161	0.03652 *
trtK:lrr.mean	-0.31256	0.11053	765.49997	-2.828	0.00481 **
trtN:lrr.mean	-0.31129	0.10190	767.26283	-3.055	0.00233 **
trtNK:lrr.mean	-0.36572	0.08749	765.25658	-4.180	0.000032498 ***
trtNP:lrr.mean	-0.13353	0.08195	765.31866	-1.629	0.10363
trtNPK:lrr.mean	-0.14534	0.07404	766.20068	-1.963	0.05002 .
trtP:lrr.mean	-0.25905	0.12032	768.48178	-2.153	0.03163 *
trtPK:lrr.mean	-0.54368	0.10256	767.07393	-5.301	0.000000151 ***

963 ---

964 Signif. codes: 0 '***', 0.001 '**', 0.01 '*', 0.05 '.', 0.1
965 , 1

966

967 Correlation of Fixed Effects:

(Intr)	trtK:.	trtN:.	trtNK:.	trtNP:.	trtNPK:.	trtP:.
trtK:lrr.mn	-0.020					
trtN:lrr.mn	-0.152	0.030				
trtNK:lrr.m	-0.165	0.031	0.101			
trtNP:lrr.m	-0.214	0.024	0.114	0.117		
trtNPK:lrr.	-0.206	0.023	0.115	0.117	0.146	
trtP:lrr.mn	-0.073	0.032	0.057	0.057	0.061	0.064
trtPK:lrr.m	-0.132	0.022	0.071	0.074	0.094	0.093

976

977

978 **Table S10.** Model averaging summaries for drivers of stability, biomass and biomass variability

979 responses.

980

981 **Stability of biomass:**

982

983 Maximum model:

984 `lrr.detr.s ~ trt + trt * (lrr.rich + lrr.sync + log.map + log.map.var) +`

985 `(1 | site_code)`

986

987 Retained fixed effects after model selection (delta <4):

	lrr.rich	lrr.sync	log.map	log.map.var	trt
988 Sum of weights:	1.00	0.93	0.28	0.24	0.07
989 N containing models:	6	5	2	2	1

991

992 Full average:

	Estimate	SE	Adj.SE	z	P
993 (Intercept)	-0.012	0.253	0.253	0.048	0.961
994 lrr.rich	0.173	0.066	0.066	2.624	0.009
995 lrr.sync	-0.032	0.017	0.017	1.944	0.052
996 log.map	-0.011	0.033	0.033	0.327	0.744
997 log.map.var	-0.004	0.027	0.027	0.142	0.887
998 trtN	-0.008	0.031	0.031	0.249	0.803
1000 trtNK	-0.009	0.034	0.034	0.255	0.799
1001 trtNP	-0.006	0.026	0.026	0.231	0.818
1002 trtNPK	-0.005	0.023	0.023	0.215	0.830
1003 trtP	-0.006	0.025	0.025	0.229	0.819
1004 trtPK	0.000	0.015	0.015	0.008	0.994

1005

1006 Conditional average:

	Estimate	SE	Adj.SE	z	P
1007 (Intercept)	-0.012	0.253	0.253	0.048	0.961
1008 lrr.rich	0.173	0.066	0.066	2.624	0.009
1009 lrr.sync	-0.035	0.015	0.015	2.383	0.017
1010 log.map	-0.039	0.054	0.054	0.735	0.463
1011 log.map.var	-0.016	0.054	0.054	0.301	0.763
1012 trtN	-0.105	0.055	0.055	1.930	0.054
1013 trtNK	-0.118	0.055	0.055	2.163	0.031
1014 trtNP	-0.080	0.055	0.055	1.467	0.142
1015 trtNPK	-0.067	0.055	0.055	1.216	0.224
1016 trtP	-0.078	0.054	0.054	1.429	0.153
1017 trtPK	-0.002	0.054	0.054	0.028	0.977

1018

1019

1020

```

1021 Mean biomass:
1022
1023 Maximum model:
1024 lrr.mean ~ trt + trt * (lrr.rich + lrr.sync + log.map + log.map.var) +
1025     (1 | site_code)
1026
1027 Retained fixed effects after model selection (delta <4):
1028           lrr.rich trt  lrr.sync log.map log.map.var
1029 lrr.rich:trt
1030 Sum of weights:      1.00      1.00 0.46      0.35      0.23      0.13
1031 N containing models:  11        11   5        5        4        3
1032
1033 Full average:
1034           Estimate SE      Adj.SE z      P
1035 (Intercept) -0.117  0.282 0.282  0.414 0.679
1036 lrr.rich -0.230  0.069 0.069  3.347 0.001
1037 trtN 0.186  0.040 0.040  4.659 0.000
1038 trtNK 0.246  0.040 0.040  6.112 0.000
1039 trtNP 0.369  0.040 0.040  9.217 0.000
1040 trtNPK 0.374  0.043 0.043  8.739 0.000
1041 trtP 0.065  0.040 0.040  1.654 0.098
1042 trtPK 0.148  0.040 0.040  3.717 0.000
1043 lrr.sync -0.007  0.010 0.010  0.661 0.509
1044 log.map 0.018  0.038 0.038  0.457 0.647
1045 log.map.var -0.003  0.026 0.026  0.110 0.913
1046 lrr.rich:trtN 0.008  0.066 0.066  0.114 0.909
1047 lrr.rich:trtNK 0.016  0.076 0.076  0.216 0.829
1048 lrr.rich:trtNP -0.002  0.061 0.061  0.036 0.971
1049 lrr.rich:trtNPK -0.038  0.115 0.115  0.330 0.742
1050 lrr.rich:trtP -0.026  0.098 0.098  0.266 0.791
1051 lrr.rich:trtPK -0.020  0.083 0.083  0.240 0.810
1052
1053 Conditional average:
1054           Estimate SE      Adj.SE z      P
1055 (Intercept) -0.117  0.282 0.282  0.414 0.679
1056 lrr.rich -0.230  0.069 0.069  3.347 0.001
1057 trtN 0.186  0.040 0.040  4.659 0.000
1058 trtNK 0.246  0.040 0.040  6.112 0.000
1059 trtNP 0.369  0.040 0.040  9.217 0.000
1060 trtNPK 0.374  0.043 0.043  8.739 0.000
1061 trtP 0.065  0.040 0.040  1.654 0.098
1062 trtPK 0.148  0.040 0.040  3.717 0.000
1063 lrr.sync -0.015  0.011 0.011  1.376 0.169
1064 log.map 0.050  0.051 0.051  0.989 0.323
1065 log.map.var -0.012  0.052 0.052  0.231 0.817
1066 lrr.rich:trtN 0.058  0.175 0.175  0.331 0.741
1067 lrr.rich:trtNK 0.126  0.175 0.175  0.720 0.471
1068 lrr.rich:trtNP -0.017  0.169 0.169  0.101 0.920
1069 lrr.rich:trtNPK -0.291  0.166 0.166  1.748 0.080
1070 lrr.rich:trtP -0.200  0.198 0.198  1.012 0.312
1071 lrr.rich:trtPK -0.154  0.181 0.181  0.847 0.397
1072
1073
1074

```

```

1075 SD of biomass:
1076
1077 Maximum model:
1078 lrr.detr.sd ~ trt + trt * (lrr.rich + lrr.sync + log.map + log.map.var) +
1079     (1 | site_code)
1080
1081 Retained fixed effects after model selection (delta <4):
1082           lrr.rich trt   log.map lrr.sync log.map.var
1083 Sum of weights:   1.00    1.00 0.43    0.38    0.27
1084 N containing models: 8        8    4        4        4
1085
1086 Full average:
1087           Estimate SE   Adj.SE z     P
1088 (Intercept) -0.235 0.485 0.486 0.484 0.628
1089 lrr.rich     -0.411 0.091 0.091 4.504 0.000
1090 trtN         0.292 0.074 0.074 3.931 0.000
1091 trtNK        0.358 0.074 0.074 4.809 0.000
1092 trtNP        0.446 0.074 0.075 5.989 0.000
1093 trtNPK       0.443 0.075 0.075 5.898 0.000
1094 trtP         0.143 0.074 0.074 1.923 0.055
1095 trtPK        0.149 0.074 0.074 2.009 0.045
1096 log.map      0.039 0.066 0.066 0.591 0.554
1097 lrr.sync     0.008 0.016 0.016 0.506 0.613
1098 log.map.var  0.001 0.040 0.040 0.026 0.980
1099
1100 Conditional average:
1101           Estimate SE   Adj.SE z     P
1102 (Intercept) -0.235 0.485 0.486 0.484 0.628
1103 lrr.rich     -0.411 0.091 0.091 4.504 0.000
1104 trtN         0.292 0.074 0.074 3.931 0.000
1105 trtNK        0.358 0.074 0.074 4.809 0.000
1106 trtNP        0.446 0.074 0.075 5.989 0.000
1107 trtNPK       0.443 0.075 0.075 5.898 0.000
1108 trtP         0.143 0.074 0.074 1.923 0.055
1109 trtPK        0.149 0.074 0.074 2.009 0.045
1110 log.map      0.091 0.074 0.074 1.232 0.218
1111 lrr.sync     0.021 0.020 0.020 1.062 0.288
1112 log.map.var  0.004 0.077 0.077 0.050 0.960
1113

```

1114 **Table S11. Model summary for nutrient treatment effects on mean species richness**

1115
 1116 Linear mixed model fit by REML. t-tests use Satterthwaite's method [
 1117 lmerModLmerTest]
 1118 Formula: lrr.rich ~ 0 + trt + (1 | site_code)
 1119 Data: lrr
 1120
 1121 REML criterion at convergence: -84.6
 1122
 1123 Scaled residuals:
 1124 Min 1Q Median 3Q Max
 1125 -5.1041 -0.5523 0.0265 0.5783 3.1723
 1126
 1127 Random effects:
 1128 Groups Name Variance Std.Dev.
 1129 site_code (Intercept) 0.00700 0.08367
 1130 Residual 0.04722 0.21731
 1131 Number of obs: 777, groups: site_code, 34
 1132
 1133 Fixed effects:
 1134 Estimate Std. Error df t value Pr(>|t|)
 1135 trtK -0.036639 0.025203 164.432341 -1.454 0.147925
 1136 trtN -0.093661 0.025203 164.432341 -3.716 0.000277 ***
 1137 trtNK -0.093698 0.025203 164.432341 -3.718 0.000275 ***
 1138 trtNP -0.121018 0.025203 164.432341 -4.802 0.000003516801 ***
 1139 trtNPK -0.169700 0.025203 164.432341 -6.733 0.000000000264 ***
 1140 trtP -0.009294 0.025203 164.432341 -0.369 0.712793
 1141 trtPK -0.067037 0.025203 164.432341 -2.660 0.008591 **
 1142 ---
 1143 Signif. codes: 0 '***', 0.001 '**', 0.01 '*', 0.05 '.', 0.1
 1144 ', 1
 1145
 1146 Correlation of Fixed Effects:
 1147 trtK trtN trtNK trtNP trtNPK trtP
 1148 trtN 0.330
 1149 trtNK 0.330 0.330
 1150 trtNP 0.330 0.330 0.330
 1151 trtNPK 0.330 0.330 0.330 0.330
 1152 trtP 0.330 0.330 0.330 0.330 0.330
 1153 trtPK 0.330 0.330 0.330 0.330 0.330 0.330
 1154

1155 **Table S12. Model summary for nutrient treatment effects on detrended species synchrony**

```

1156 Linear mixed model fit by REML. t-tests use Satterthwaite's method [
1157 lmerModLmerTest]
1158 Formula: lrr.sync ~ 0 + trt + (1 | site_code)
1159 Data: lrr
1160
1161 REML criterion at convergence: 2265
1162
1163 Scaled residuals:
1164   Min       1Q   Median       3Q      Max
1165 -4.2103 -0.6279  0.0262  0.6445  2.8514
1166
1167 Random effects:
1168   Groups      Name                Variance Std.Dev.
1169   site_code (Intercept) 0.2244   0.4737
1170   Residual                0.9839   0.9919
1171 Number of obs: 777, groups:  site_code, 34
1172
1173 Fixed effects:
1174           Estimate Std. Error      df t value Pr(>|t|)
1175 trtK      -0.03914    0.12472 119.96988  -0.314  0.7542
1176 trtN       0.08092    0.12472 119.96988   0.649  0.5177
1177 trtNK     -0.23001    0.12472 119.96988  -1.844  0.0676 .
1178 trtNP     -0.11916    0.12472 119.96988  -0.955  0.3413
1179 trtNPK    -0.14591    0.12472 119.96988  -1.170  0.2444
1180 trtP      -0.11947    0.12472 119.96988  -0.958  0.3400
1181 trtPK     -0.09823    0.12472 119.96988  -0.788  0.4325
1182 ---
1183 Signif. codes:  0 , '***', '0.001', '**', '0.01', '*', '0.05', '.', '0.1
1184 , '0.5', '1'
1185
1186 Correlation of Fixed Effects:
1187           trtK  trtN  trtNK  trtNP  trtNPK  trtP
1188 trtN      0.430
1189 trtNK     0.430 0.430
1190 trtNP     0.430 0.430 0.430
1191 trtNPK    0.430 0.430 0.430 0.430
1192 trtP      0.430 0.430 0.430 0.430 0.430
1193 trtPK     0.430 0.430 0.430 0.430 0.430 0.43
1194

```

1195 **Table S13.** Summary of author contributions and site-level acknowledgments. Site names match those in Table S1.

Name	Site(s) used in analysis	Developed /framed research question(s)	Analyzed data	Contributed to data analyses	Wrote the paper	Contributed to paper writing	Site co-ordinator	Nutrient Network co-ordinator	Site acknowledgements
Oliver Carroll		x	x		x				
Evan Batzer				x		x			
Siddharth Bharath				x		x			
Elizabeth T. Borer	cdcr.us, bnch.us, look.us, hopl.us, mcla.us, sier.us					x	x	x	
Sofia Campana						x			
Ellen H. Esch				x		x			
Yann Hautier	frue.ch			x		x	x		
Timothy Ohlert	sevi.us			x		x	x		
Eric W. Seabloom	cdcr.us, bnch.us, look.us, hopl.us, mcla.us, sier.us			x		x	x	x	
Peter B. Adler	shps.us					x	x		
Jonathan D. Bakker	smith.us					x	x		
Lori Biederman	cbgb.us					x	x		
Miguel N. Bugalho	comp.pt					x	x		MNB was funded by FCT contracts DL 57/2016/CP1382/CT0030, UID/BIA/ 50027/2013 and POCI-01-0145-FEDER
Maria Caldeira	comp.pt					x	x		Funding for CEF (UID/AGR /00239/2019) and Companhia das Lezirias for site access
Qingqing Chen						x			
Kendi Davies	bldr.us					x	x		
Philip A. Fay	temple.us					x	x		
Johannes M. H. Knopps	cdrp.us					x	x		
Kimberly Komatsu	konz.us, saline.us					x	x		
Jason Martina	temple.us					x	x		
Kevin S. McCann				x		x			
Joslin L. Moore	bogong.au					x	x		
John W. Morgan	bogong.au, kiny.au					x	x		

Table S13. Continued.

Name	Site(s) used in analysis	Developed /framed research question(s)	Analyzed data	Contributed to data analyses	Wrote the paper	Contributed to paper writing	Site co-ordinator	Nutrient Network co-ordinator	Site acknowledgements
Taofeek O. Muraina						X			
Brooke Osborne						X			
Anita C. Risch	valm.ch					X	X		
Carly Stevens	lancaster.uk					X	X		
Peter A. Wilfhart						X		X	
Laura Yahdjian						X	X		
Andrew S. MacDougall	cowi.ca	X				X	X		

1196

1197

1198 **Table S14.** Principal investigators of sites from which data were used in this analysis, but who are
 1199 not authors. Names ordered by site. Data they provided was critical to this work.

Site PI	Site code
Brett Melbourne	bldr.us
Jennifer Firn	burrawan.au
W. Stanley Harpole, Kirsten Hofmockel, Lauren Sullivan	cbgb.us
W. Stanley Harpole	cdcr.us
Elsa Cleland	elliott.us
Andy Hector	frue.ch
Rebecca McCulley, Jim Nelson	hall.us
W. Stanley Harpole	hopl.us
Mahesh Sankaran	kibber.in
Marc Cadotte, Arthur Weiss	koffler.ca
Melinda Smith	konz.us
Juan Alberti, Pedro Daleo	marc.ar
W. Stanley Harpole	mcla.us
Suzanne Prober	mtca.au
Melinda Smith	saline.us
Carka D'Antonio, W. Stanley Harpole	sedg.us
Scott Collins, Laura Ladwig	sevi.us
Dana Blumenthal, Cynthia Brown, Julia Klein, Alan Knapp	sgs.us
W. Stanley Harpole	sier.us
Janneke Hille Ris Lambers	smith.us
Rebecca McCulley, Jim Nelson	spin.us
Xiaohui Feng, Andrew Leakey	trel.us
Kevin Kirkman, Michelle Tedder	ukul.za
Martin Schuetz	valm.ch