

1 **Out of the shadows: multiple nutrient limitation drives relationships between biomass,**
 2 **light, and plant diversity**

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49

50 **Abstract:**

51 The paradigmatic hypothesis for the effect of fertilisation on plant diversity represents a one-
52 dimensional tradeoff for plants competing for belowground nutrients (generically) and
53 aboveground light: fertilisation reduces competition for nutrients while increasing biomass and
54 thereby shifts competition for depleted available light. The essential problem of this simple
55 paradigm is that it misses both the multivariate and mechanistic nature of the factors that
56 determine biodiversity as well as their causal relationships. We agree that light limitation, as
57 DeMalach and Kadmon argue, can indeed be an important factor associated with diversity loss,
58 and we presented it as an integral part of our tests of the niche dimension hypothesis. We
59 disagree with DeMalach and Kadmon that light is the “main” factor explaining diversity, because
60 this misrepresents the causal structure represented in the design of our experiment in which
61 multiple nutrient addition was the ultimate causal driver of a suite of correlated responses that
62 included diversity and light, and especially live and dead biomass, which are the factors that
63 control light depletion. Our findings highlight that multiple nutrient limitation can structure plant
64 diversity and composition independently of changes in light and biomass. For example,
65 approximately one third of our sites showed no significant increase in biomass with greater
66 number of added nutrients yet still lost diversity when nutrients were added. The important
67 message is that while light limitation can be an important contributor to diversity loss, it is not a
68 necessary mechanism.

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71

72 **Text:**

73 *“Men throw huge shadows on the lawn, don't they? Then, all their lives, they try to run to fit*
74 *the shadows”* — Ray Bradbury

75

76 DeMalach and Kadmon (this issue; abbreviated D&K hereafter) reanalysed our experimental
77 data (Harpole et al. 2016) with the goal to disentangle two hypotheses that can explain loss of
78 plant diversity due to multiple resource addition: the light asymmetry hypothesis and the niche
79 dimension hypothesis (Harpole et al. 2016). D&K *“conclude that current knowledge provides a*
80 *strong support for the light-asymmetry hypothesis and no support for the niche dimension*
81 *hypothesis”*. We disagree. It has been widely demonstrated that fertilisation can reduce plant
82 diversity through a one-dimensional tradeoff for plants: fertilisation reduces competition for
83 nutrients belowground while increasing plant biomass and thereby increases competition for
84 depleted available light aboveground (Newman 1973; Hautier et al. 2009; Borer et al. 2014a; but
85 see Grime 1973). Accordingly, we agree with D&K that light limitation can be an important
86 factor associated with diversity loss. Indeed, light limitation is an integral part of our tests of the
87 niche dimension hypothesis (Harpole & Tilman 2007; Harpole et al. 2016): *“Our results suggest*
88 *that a combination of a decreased number of limiting resources and changes in the identity of*
89 *limiting factors (e.g., light) resulting from indirect effects of productivity led to decreased niche*
90 *dimension and diversity.”* (Harpole & Tilman 2007, p. 793).

91

92 We welcome this chance to clarify aspects of our multi-dimensional hypothesis that may not
93 have been entirely clear in our original, shorter-format manuscript. We start by specifically
94 addressing D&K's five core criticisms of our test of the niche dimension hypothesis, which

95 mainly reiterate caveats and limitations we had presented in our own discussion (Harpole et al.
96 2016). We then provide a more detailed outline of the conceptual background and experimental
97 tests of the niche dimension hypotheses and the evidence we used to support our conclusion
98 multiple nutrient addition can directly drive changes in diversity, while simultaneously and
99 independently affecting diversity through the indirect effects of nutrients driving changes in live
100 and dead biomass and light depletion. Lastly, because we are in complete agreement with D&K
101 about the importance of light for aboveground plant competition—that is not the debate—we
102 address the problematic assumptions and logic underlying D&K’s comments.

103

104 *Addressing D&K’s criticisms of Harpole et al. 2016:*

105

106 1) D&K stated that “*while experimental demonstration of these patterns does indicate a causal*
107 *relationship between resource addition and species loss (or compositional divergence), it*
108 *does not tell us anything about the mechanisms underlying these patterns.*” We completely
109 agree and we stated this: “*Stronger tests of the role of multiple resource competition for*
110 *structuring species coexistence require physiological studies quantifying species-specific*
111 *functional traits and trade-offs, and testing whether species respond to resource treatments*
112 *similarly in different environments. Deeper mechanistic insight can also be gained by asking*
113 *how resource-dependent diversity patterns and mechanisms change across scales (for*
114 *example, from local to regional) in response to global change drivers such as nutrient*
115 *pollution. Our results point to, but do not distinguish among, the presumed resource*
116 *competition mechanisms that underlie the resource dimension hypothesis*” (Harpole et al.
117 2016). While we manipulated the number of added nutrients and showed that the number of

118 nutrients drove changes in species diversity and composition in multiple ways that are
119 consistent with the niche dimension hypotheses, a deeper-level mechanistic explanation is
120 clearly a needed future research topic, which we pointed to (Harpole et al. 2016).

121 2) D&K argued that the “*concept of discrete ‘number’ of limiting resources is too simplistic and*
122 *should be replaced by more realistic concepts of co-limitation by multiple essential elements*”

123 . We agree that the essence of Hutchinson’s 1957 prediction is simplistic—it was a
124 geometric-based concept to make a simple but elegant argument (Hutchinson 1957).
125 Nevertheless, this represents a 60 year-old prediction, which has only been tested and
126 supported by a handful of studies in the past decade. Our motivation was to test the
127 generality of this basic ecological prediction and explore the potential variability of multiple
128 resource-diversity relationships across 45 grassland sites around the world. There is no
129 question that Hutchinson’s conceptual presentation of the niche dimension hypothesis needs
130 greater development in terms of mechanism and realism. In fact, we have discussed
131 extensively the realism of co-limiting nutrients (Harpole et al. 2011; Fay et al. 2015), and we
132 also stated that: “*Estimating effective upper bounds on ecologically relevant resource*
133 *dimensionality will depend on the degree to which multiple limiting factors covary, how they*
134 *change in time and space, and how multiple limiting factors interact with each other in*
135 *promoting coexistence*” (Harpole et al 2016).

136 3) D&K argued that because sites (approximately one third of 45 sites) where community
137 biomass did not increase with added nutrients, nutrients were therefor not limiting and could
138 not affect diversity. But they missed the logic and the point we made that although
139 community biomass is the standard response variable for assessing nutrient limitation,

140 multiple processes, from individual physiology to ecosystem-level, can be limited by
141 multiple nutrients, and, importantly, *that different processes can be limited by different*
142 *nutrients* (Harpole et al. 2016; and discussed extensively in Harpole et al. 2011). We also
143 pointed to multiple alternative mechanisms whereby changes in nutrient availability might
144 negatively affect diversity indirectly: e.g., changes in other limiting factors including light,
145 soil water and herbivory.

146 4) D&K criticise our experimental design for only adding soil nutrients, and that because “*light*
147 *supplementation was kept constant*” (because it was not directly manipulated), the number
148 and the type of resource limitation was confounded. Expressed more precisely, what we said
149 previously was: “*Environmental change can therefore reduce the niche dimension of*
150 *particular ecological communities through decreases in the number or heterogeneity of*
151 *limiting resources or through changes in the identity and stoichiometry of limiting resources*”
152 (Harpole & Tilman 2007). In other words, there are at least four interrelated mechanisms
153 underlying the niche dimension hypothesis. As we also highlighted and have explored
154 elsewhere (Cardinale et al. 2009), the total amount of resources and their ratios were also not
155 experimentally independent, but these components are not exclusive and all are integral to the
156 niche dimension hypothesis. We agree with D&K that these issues and others that we
157 discussed (such as nutrient fertilisers being made of multi-element salts and that individual
158 elements are often available in different molecular forms) make quantification of effective
159 dimensionality challenging. Our purpose was to test for the generality of evidence that would
160 be consistent with multi-dimensional resource niches, within the constraints of a globally-
161 distributed factorial experiment that necessarily traded off the experimental design
162 parameters of number of sites, replication within sites, treatment factor number and levels,

163 and feasibility in terms of cost and sampling effort (Borer et al. 2014b). There is no question
164 that there remain numerous questions and mechanisms to explore and we stand by our
165 conclusion: “*Our results point to the importance of understanding dimensionality in*
166 *ecological systems that are undergoing diversity loss in response to multiple global change*
167 *factors.*”

168 5) D&K form a different conclusion about the alternative mechanisms we explored in testing
169 support for the niche dimension hypothesis. They misunderstand the multivariate aspect of
170 our study: the mechanisms we discussed whereby multiple nutrient limitations structure
171 diversity are not alternative in the mutually-exclusive sense they claim, but they are expected
172 to act simultaneously. Furthermore, we presented evidence that niche dimensionality is a
173 novel and overlooked mechanism that can act *in addition* to the traditionally invoked
174 mechanism whereby nutrient addition increases biomass and litter and reduces light, which
175 thereby may all *indirectly* contribute to diversity loss. These are not mutually-exclusive. The
176 question of the relative strength of these direct and indirect consequences of eutrophication in
177 co-limited systems is a valid one but needs to be understood in the context of a multivariate
178 framework that also acknowledges other mechanisms that may not be included. This last
179 criticism appears to us to contain the essence of the misunderstanding of D&K about the
180 purpose and design of our experiments and our results; we focus the remainder of our
181 response on these aspects.

182

183 *Ultimate versus proximate causes:*

184 D&K demonstrate a fundamental misunderstanding of the causality and response
185 relationships underlying our experimental design in their suggestion that light limitation is the “
186 main factor” driving diversity loss (Borer et al. 2014b; Oehlert 2010). Our results derive from an
187 experiment in which the independent factors (i.e., the *treatments*) were the number and
188 combinations of added nutrients (N, P, K and micronutrients) (Fig. 1). Quite simply, nutrients
189 were, by design, the underlying causal drivers. The dependent variables (i.e., the *responses*)
190 included several diversity metrics, live and dead aboveground biomass, and light, all of which
191 were correlated (Fig. 1b). Site-level species pools and number of years of treatment were
192 *covariates*. In the context of a controlled experiment in which light is a response, the claim of
193 D&K that “*light competition is the main factor explaining species loss*” diversity loss is neither
194 logical nor statistically supportable (Fig. 1c). In other words, light might act as a proximate factor
195 affecting diversity, but any effect of light must be the indirect consequence of the ultimate causal
196 factors of our experimental design—the addition of multiple resources. Assessing the direct
197 causal role of light limitation for diversity, and its importance relative to other predictors, would
198 require a different approach, such as experimentally, and independently, increasing light below
199 the plant canopy, thereby reversing the light limitation caused by nutrient addition (see Hautier et
200 al. 2009). Unfortunately, the example given by DeMalach et al. (2017) examined the influence of
201 light only indirectly, and confounded multiple effects with manipulation of competition.

202

203 D&K therefore misapplied the multiple regression model that we originally presented as a
204 heuristic illustration of the existing paradigm of diversity loss resulting from nutrient addition. In
205 other words, Harpole et al. (2016) used that linear model simply to show that residual variation in
206 plant diversity could still be explained by the number of added resources, after controlling for

207 variation in the traditional or paradigmatic explanatory variables (e.g., live and dead biomass, and
208 light) (Harpole et al. 2016). We used that model to ask the question, is there support for including
209 niche dimensionality as a mechanism that might act independent of, and in addition to, the
210 standard biomass-related mechanisms (Fig. 1b)? The model is technically incorrect because live
211 and dead biomass and light are dependent variables and correlated, violating assumptions of
212 linear regression, but we used the model as an “added variable” test that provided just one of a
213 number of lines of evidence that we used to support our conclusions. However, D&K next used
214 the standardised multiple regression coefficients from that model to conclude that light was the “
215 *main factor explaining diversity loss*” and that the actual experimental treatment factors—
216 multiple added nutrients—were unimportant and that therefor there was “*no support for the niche*
217 *dimension hypothesis*” (D&K this issue). They further suggested that the effects of nutrients were
218 exaggerated because they were “*measured without variance*”—a misunderstanding of the design
219 because they were factor level treatments (Oehlert 2010). To highlight the logical and conceptual
220 problems with their approach, we examined their methods further. What D&K omitted from the
221 presentation of their analysis were the other variables in their model: the number of years of
222 treatment, the site species pool and total plant species cover, all important aspects of the
223 experiment and our questions. The standardised coefficients for these omitted variables show
224 species pool sizes and the number of years of treatment to be much larger than that for light (Fig.
225 2a). By selecting only the “main” variable having the largest coefficient, as D&K advocate, then
226 light as an explanation would be rejected. But, this would be the wrong conclusion and for the
227 wrong reason.
228

229 Is light important? Yes, we agree completely with D&K and we showed that it was: “We
230 *found that increasing the number of added resources increased live biomass..., and decreased*
231 *the proportion of photosynthetically active radiation (PAR) transmitted through the canopy to the*
232 *ground surface”* (Harpole et al. 2016, p. 94). But changes in light depletion are just part of the
233 multivariate suite of correlated responses that include live and dead biomass, total cover and
234 species composition. Also potentially important are changes to variables we were not able to
235 measure, e.g., physiology, allocation and traits; soil moisture, air temperature and humidity;
236 herbivory, pathogens, and mutualists; spatial heterogeneity and temporal changes in community
237 dynamics; and ecosystem processes. However, we can still ask what is the relationship between
238 light depletion and diversity if we properly account for added nutrients as the *independent*
239 variables, years of treatment and species pools as *covariates*, and diversity, live and biomass,
240 cover and light as the set of correlated *response* variables (Fig. 1)? Here, correlations are the
241 more reasonable way to describe the relationships among this last set of variables because
242 causality can go both ways.

243

244 To explore the relationships between diversity and live and dead biomass (log-transformed),
245 cover, and light (the *responses*), we quantified, for each, the residuals after controlling for the
246 independent variables – both the effects of factorial addition of N, P and K+ μ (the *treatments*),
247 and species pool size and number of treatment years (the *covariates*), and the random variation
248 associated with blocking factors (Fig. 1). After accounting for these effects, most response (i.e.,
249 *dependent*) variables remained significantly correlated with each other (Fig. 2b). Together, the
250 independent variables explained 52% of variation in diversity. The remaining (*residual*) variation
251 in diversity was positively and significantly correlated with light, but with an r^2 of only 0.017

252 (Fig. 2b, $r=0.13$). The bottom line is that multiple nutrient addition and larger-scale diversity are
253 the main explanatory variables for the response of diversity in this experimental study. Then,
254 what might be the role of light, as a response and a potential proximate casual factor, within a
255 niche dimensional framework?

256

257 *Conceptual illustration of the multi-dimensional niche:*

258 Central to Hutchinson's (1957) niche dimension hypothesis is the assumption that niches are
259 multivariate. If multiple factors constrain species (i.e., their number, relative abundances and
260 productivity, etc.), then changes to those factors should drive changes in diversity and other
261 variables. Multiple resource limitation has been shown to be common and often synergistic, with
262 multiplicative interactions between resources (see Elser et al. 2007; Harpole et al. 2011; Fay et al.
263 2015). In a global study of nutrient limitation for N, P, and K, for example, Fay et al. (2015)
264 found that *ca.* 25% of the sites studied were not primarily limited by any nutrient, while the
265 remainder of sites showed different sensitivities to the single or interacting influences of
266 combinations of the nutrients. While the scale of comparison here was primarily among sites, it
267 made the point that resource limitation is very much a multivariate and context-dependent
268 process, which can shape fundamental processes of niche evolution and species coexistence.
269 Indeed, Hutchinson's logic that the number of species should increase with the number of niches
270 was simply an inversion and extension of Gause's competitive exclusion principle (Gause 1934);
271 for two species competing for only one limiting resource there can be only one winner at
272 equilibrium. It follows that if species coexistence is partly dependent on tradeoffs for multiple
273 limiting factors, then greater numbers of limiting resources should promote greater species
274 diversity (Levin 1970). It also follows that if resources were to be made non-limiting (by adding

275 them in excess), that there should be fewer tradeoff possibilities for *those species adapted to and*
276 *coexisting under the original conditions*; competition occurs for limiting, not non-limiting factors
277 (Harpole & Tilman 2007).

278

279 More precisely, this *niche dimension* hypothesis predicts that “*Environmental change can*
280 *therefore reduce the niche dimension of particular ecological communities through decreases in*
281 *the number or heterogeneity of limiting resources or through changes in the identity and*
282 *stoichiometry of limiting resources*” (Fig. 3; Harpole & Tilman 2007, p. 791). Thus, addition of
283 limiting resources should lead to loss of species diversity generally, but this effect will depend
284 critically on how the “balance” or stoichiometry of the limiting resources (including light and
285 many other factors) changes (Cardinale et al. 2009; Lewandowska et al. 2016). In some cases we
286 might expect addition of particular combinations of resources to restore a balanced supply of
287 resources that promotes coexistence, which is the mechanism that Hautier et al. (2009) found
288 when they experimentally added light back to the understory of fertilised communities, refuting
289 the interpretation of D&K (this issue and 2017). The consequences of altered resource supply
290 also depend on the relationships between the pool of species present, the multivariate set of traits
291 and tradeoffs they represent, and how these map onto multivariate resource supply clouds (Fig.
292 3). However, because there are practical limits to the number of factors that can be tested in one
293 experiment, we focused on combinations of three nutrient resource treatments. We acknowledged
294 though that other factors are important in structuring diversity and these can interact with
295 resources, such as micronutrients and toxins, soil properties including pH, pathogens and
296 specialised herbivores. Given that changes in nutrient supply can drive complex relationships

297 among environmental factors, our observation that light limitation is an important but not a
298 necessary driver of diversity loss should not be controversial.

299

300 By promoting light asymmetry as their main explanation for the negative effects of nutrients
301 on diversity, D&K ignore evidence showing that the effects of light depletion are not always
302 negative. Shading can have positive effects on diversity, including when facilitating plant
303 recruitment in moisture-stressed environments (e.g., Carson and Pickett 1990; Dickson and
304 Foster 2011; Richardson et al. 2012). We showed elsewhere how nutrient addition negatively
305 affects soil moisture (Harpole et al. 2007), and water and nitrogen generally co-limit plant
306 communities across a wide range of precipitation (Eskelinen & Harrison 2015; Hooper and
307 Johnson 1999). Therefore, addition of multiple nutrient resources need not necessarily shift
308 competition to aboveground light but can shift the identity of limiting resources to an alternative
309 belowground resource such as water (for example, see Simkin et al. 2016). Changes in resources
310 can also change trophic relationships, which are often as or more important than limiting
311 resources (Borer et al. 2014a). Nutrient addition can change rates of herbivory by changing the
312 quantity and quality of plant tissue and drive changes in the relative abundance of species that
313 differ in their susceptibility, defenses and responses to different consumers; herbivores, in turn,
314 can contribute to the maintenance of diversity by stabilizing plant community evenness
315 (Mortensen et al. 2017). And, we must remember that these are grassland ecosystems that are
316 strongly defined by grazers and water availability (Frank et al. 1998).

317

318 *Summary:*

319 Our findings highlighted that multiple nutrient limitation can structure plant diversity and
320 composition independently of changes in biomass and light. Approximately one third of our sites
321 showed no significant increase in biomass with greater number of added nutrients, yet these sites
322 still lost diversity when nutrients were added and composition changed in ways consistent with
323 species' tradeoffs for different limiting resources (Harpole et al. 2016). The important message
324 was that while light limitation can be an important contributor to diversity loss, it is not the only
325 or even a necessary mechanism. But the essential issue here is whether attempting to identify a
326 single "main" factor is adequate or insightful to explain complex ecological phenomena; we
327 contend it is not. D&K's misrepresentation of causality only distracts from progress towards
328 understanding the multivariate drivers of diversity. Furthermore, the question that is left open by
329 D&K is that even if fertilized plots lose diversity mainly due to light competition, this says
330 nothing about how diversity was maintained in the unfertilized plots that were limited by multiple
331 nutrients and presumably not limited by light. The light asymmetry hypothesis does not help us
332 understand the maintenance of diversity in plant communities where nutrients have not been
333 added. In addition, because we experimentally manipulated nutrients, not light, a direct light x
334 nutrient manipulation experiment would be necessary for a true comparison of these mechanisms
335 and their interactions. We reiterate our call to work towards multivariate and mechanistic
336 experiments and models for plant diversity that integrate the multiple mechanisms that have been
337 demonstrated in natural systems (Grace et al. 2016). There is much more to plant communities
338 than the shadows on the lawn.

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Data Accessibility: All data and supporting information used in this manuscript were presented in Harpole et al. 20016, the subject of this comment article.

References:

- Borer, E. T., Seabloom, E. W., Gruner, D. S., Harpole, W. S., Hillebrand, H., Lind, E. M., et al. (2014a). Herbivores and nutrients control grassland plant diversity via light limitation. *Nature*, **508**(7497), 517-20.
- Borer, E. T., Harpole, W. S., Adler, P. B., Lind, E. M., Orrock, J. L., Seabloom, E. W., et al. (2014b). Finding generality in ecology: A model for globally distributed experiments. *Methods in Ecology and Evolution*, **5**(1), 65-73.
- Cardinale, B. J., Hillebrand, H., Harpole, W. S., Gross, K., & Ptacnik, R. (2009). Separating the influence of resource 'availability' from resource 'imbalance' on productivity–diversity relationships. *Ecology Letters*, **12**, 475-487.
- Carson, W. P. & Pickett, S. T. A. (1990). Role of resources and disturbance in the organization of an old-field plant community. *Ecology*, **71**(1), 226-238.
- DeMalach, N., Zaady, E., & Kadmon, R. (2017). Light asymmetry explains the effect of nutrient enrichment on grassland diversity. *Ecology Letters*. **20**, 60-69.
- Dickson, T. L. & Foster, B. L. (2011). Fertilization decreases plant biodiversity even when light is not limiting. *Ecology Letters*, **14**(4), 380-8.
- Elser, J. J., Bracken, M. E. S., Cleland, E. E., Gruner, D. S., Harpole, W. S., Hillebrand, H., et al. (2007). Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecology Letters*, **10**(12), 1135-42.
- Eskelinen, A. & Harrison, S. P. (2015). Resource colimitation governs plant community responses to altered precipitation. *Proceedings of the National Academy of Sciences of the United States of America*, **112**, 13009-13014.
- Fay, P. A., Prober, S. M., Harpole, W. S., Knops, J. M. H., Bakker, J. D., Borer, E. T., et al. (2015). Grassland productivity limited by multiple nutrients. *Nature Plants*, **1**, 15080-.
- Frank, D. A., McNaughton, S. J., & Tracy, B. F. (1998). The ecology of the earth's grazing ecosystems. *BioScience*, **48**(7), 513-521.
- Gause, G. F. (1934). Experimental analysis of Vito Volterra's mathematical theory of the struggle for existence. *Science*, **79**(16-17), 340.
- Grace, J. B., Anderson, T. M., Seabloom, E. W., Borer, E. T., Adler, P. B., Harpole, W. S., et al. (2016). Integrative modelling reveals mechanisms linking productivity and plant species richness. *Nature*, **529**(7586), 390-393.

- Grime, J. P. (1973). Competition and diversity in herbaceous vegetation (reply). *Nature*, **244**, 311.
- Harpole, W. S. & Tilman, D. (2007). Grassland species loss due to reduced niche dimension. *Nature*, **446**, 791-793.
- Harpole, W. S., Ngai, J. T., Cleland, E. E., Seabloom, E. W., Borer, E. T., Bracken, M. E., et al. (2011). Nutrient co-limitation of primary producer communities. *Ecology Letters*, **14**, 852-862.
- Harpole, W. S., Potts, D. L., & Suding, K. N. (2007). Ecosystem responses to water and nitrogen amendment in a California grassland. *Global Change Biology*, **13**, 1-8.
- Harpole, W. S., Sullivan, L. L., Lind, E. M., Firn, J., Adler, P. B., Borer, E. T., et al. (2016). Addition of multiple limiting resources reduces grassland diversity. *Nature*, **537**(7618), 93-96.
- Hautier, Y., Niklaus, P. A., & Hector, A. (2009). Competition for light causes plant biodiversity loss after eutrophication. *Science*, **324**(5927), 636-8.
- Hooper, D. U. & Johnson, L. (1999). Nitrogen limitation in dryland ecosystems: Responses to geographical and temporal variation in precipitation. *Biogeochemistry*, **46**, 247-293.
- Hutchinson, G. E. (1957). Concluding remarks. *Quantitative Biology*, **22**, 415-427.
- Levin, S. A. (1970). Community equilibria and stability, and an extension of the competitive exclusion principle. *American Naturalist*, **104**, 413-423.
- Lewandowska, A. M., Biermann, A., Borer, E. T., Cebrián-Piqueras, M. A., Declerck, S. A. J., Meester, L. D., et al. (2016). The influence of balanced and imbalanced resource supply on biodiversity–functioning relationship across ecosystems. *Phil. Trans. R. Soc. B*, **371**(1694), 20150283.
- Mortensen, B., Danielson, B., Harpole, W. S., Alberti, J., Arnillas, C. A., Biederman, L., Borer, E. T., Cadotte, M. W., Dwyer, J. M., Hagenah, N., Hautier, Y., Peri, P. L., and Seabloom, E. W. (2017). Herbivores safeguard plant diversity by reducing variability in dominance. *Journal of Ecology*. doi 10.1111/1365-2745.12821
- Newman, E. I. (1973). Competition and diversity in herbaceous vegetation. *Nature*, **244**, 310.
- Oehlert, G. W. (2010). *A first course in design and analysis of experiments*. W.H. Freeman.
- Richardson, P. J., MacDougall, A. S., Stanley, A. G., Kaye, T. N., & Dunwiddie, P. W. (2012). Inversion of plant dominance--diversity relationships along a latitudinal stress gradient. *Ecology*, **93**(6), 1431-1438.
- Simkin, S. M., Allen, E. B., Bowman, W. D., Clark, C. M., Belnap, J., Brooks, M. L., et al. (2016). Conditional vulnerability of plant diversity to atmospheric nitrogen deposition across the United States. *Proceedings of the National Academy of Sciences*, **113**(15), 4086-4091.

Figure Legends:

Figure 1.

a) Illustration of our experimental design at each of the 45 grassland sites in this study (map). We applied factorial combinations of P, N, and K plus micronutrients (μ)—the treatments—to plots as indicated by the blue, yellow and red boxes around each plot. Species are indicated by colored points corresponding to the nutrients for which they are best competitors when those nutrients are scarce. Random variation was accounted for by considering three covariates: the species pool of the site, spatial blocks, and the number of years of nutrient addition (shown in dashed boxes). Responses were measured as a suite of correlated variables (shown in dotted boxes, and labeled with italic font). Different nutrients drove different changes in community composition and greater number of added resources drove greater loss of diversity. Nutrient addition also tended to increase live and dead biomass, which was associated with a decrease in photosynthetically active radiation (PAR) at the ground surface. b, c) Contrasting conceptual frameworks of b) Harpole et al. (2016): Multiple nutrient addition drives a suite of correlated responses, including diversity and light (ultimate causal factors shown by bold solid arrows; response variables and potential proximate causal relationships shown as curved, dotted arrows). c) D&K (this issue) tested the relative effects of live and dead biomass, light and nutrients as independent and direct drivers of diversity.

Figure 2.

a) Re-created plot from D&K showing the relative sizes of the standardised coefficients of the response variables live and dead biomass, PAR (light) and the independent variables the number of added resources (means +/- standard error in black). The variables in the model

omitted from the plot by D&K were the number of years of nutrient addition, site-level species pool size estimates, and total cover (means +/- standard error in red). The magnitudes of years of treatment and species pool are greater than that for light. But, see text for further explanation of why this model is inappropriate.

b) After accounting for variation due to treatment factors (added resources) and covariates (block, years of treatment, species pool), the response variables (live and dead biomass, light, cover, and diversity) remain correlated. The diagonal panels show the distribution of each response variables after controlling for treatments and covariates; the panels in the lower triangle show the scatterplot and smoothed fit (in red); the panels in the upper triangle show the correlation coefficient (r , in bold if significant after multiple comparison correction). To aid interpretation, the panels relating light and diversity are highlighted in yellow.

Figure 3.

Resource addition can reduce the niche dimension of particular ecological communities by decreasing the i. number, ii. stoichiometry, iii. identity, or iv. heterogeneity of limiting resources (Harpole & Tilman 2007). a) Species competing through tradeoffs in their minimum requirements for three resources (R1, R2, R3). The grey plane represents the tradeoff surface. Addition of R1 (yellow arrow) shifts the resource supply away from the ambient conditions (light grey ellipse) to a region where R1 is no longer limiting (yellow ellipse) and causes loss of those species (yellow) that are best competitors for that resource when it is scarce. Addition of R1 thus indicated a change in the number of limiting resources, as well as changes in the heterogeneity and stoichiometry (e.g., R1:R2 and R1:R3). b) Addition of R2 (blue) decreases the number of limiting resources again, and shifts the stoichiometry towards resource regions favoring species that are

better competitors for R3 (red) or increases relative limitation by another factor (dashed third axis). c) Addition of R3 pushes the system to limitation by another factor R4 (change in identity).