

COMMENTARY

Out of the shadows: multiple nutrient limitations drive relationships among biomass, light and plant diversity

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Summary

1. The paradigmatic hypothesis for the effect of fertilisation on plant diversity represents a one-dimensional trade-off for plants competing for below-ground nutrients (generically) and above-ground light: fertilisation reduces competition for nutrients while increasing biomass and thereby shifts competition for depleted available light.
2. The essential problem of this simple paradigm is that it misses both the multivariate and mechanistic nature of the factors that determine biodiversity as well as their causal relationships.
3. We agree that light limitation, as DeMalach and Kadmon argue, can indeed be an important factor associated with diversity loss, and we presented it as an integral part of our tests of the niche dimension hypothesis.
4. We disagree with DeMalach and Kadmon that light is the ‘main’ factor explaining diversity, because this misrepresents the causal structure represented in the design of our experiment in which multiple nutrient addition was the ultimate causal driver of a suite of correlated responses that included diversity and light, and especially live and dead biomass, which are the factors that control light depletion.

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5. Our findings highlight that multiple nutrient limitations can structure plant diversity and composition independently of changes in light and biomass. For example, approximately one-third of our sites showed no significant increase in biomass with greater number of added nutrients yet still lost diversity when nutrients were added.

6. The important message is that while light limitation can be an important contributor to diversity loss, it is not a necessary mechanism.

Key-words: biodiversity, light, multivariate causal relationships, nutrient limitation, resource limitation

Men throw huge shadows on the lawn, don't they? Then, all their lives, they try to run to fit the shadows'

– Ray Bradbury

DeMalach & Kadmon (2017; abbreviated D&K hereafter) reanalysed our experimental data (Harpole *et al.* 2016) with the goal to disentangle two hypotheses that can explain loss of plant diversity due to multiple resource addition: the light asymmetry hypothesis and the niche dimension hypothesis (Harpole *et al.* 2016). D&K 'conclude that current knowledge provides a strong support for the light-asymmetry hypothesis and no support for the niche dimension hypothesis'. We disagree with the D&K conclusion. It has been widely demonstrated that fertilisation can reduce plant diversity through a one-dimensional trade-off for plants: fertilisation reduces competition for nutrients below-ground while increasing plant biomass and thereby increases competition for depleted available light above-ground (Newman 1973; Hautier, Niklaus & Hector 2009; Borer *et al.* 2014b; but see Grime 1973). Accordingly, we agree with D&K that light limitation can be an important factor associated with diversity loss. Indeed, light limitation is an integral part of our tests of the niche dimension hypothesis (Harpole & Tilman 2007; Harpole *et al.* 2016): 'Our results suggest that a combination of a decreased number of limiting resources and changes in the identity of limiting factors (e.g., light) resulting from indirect effects of productivity led to decreased niche dimension and diversity' (Harpole & Tilman 2007, p. 793).

We welcome this chance to clarify aspects of our multidimensional hypothesis that may not have been entirely clear in our original, shorter format manuscript. We start by specifically addressing D&K's five core criticisms of our test of the niche dimension hypothesis, which mainly reiterate caveats and limitations we had presented in our own discussion (Harpole *et al.* 2016). We then provide a more detailed outline of the conceptual background and experimental tests of the niche dimension hypotheses and the evidence we used to support our conclusion multiple nutrient addition can directly drive changes in diversity, while simultaneously and independently affecting diversity through the indirect effects of nutrients driving changes in live and dead biomass and light depletion. Lastly, because we are in complete agreement with D&K about the importance of light for above-ground plant competition – that is not the debate – we address the problematic assumptions and logic underlying D&K's comments.

ADDRESSING D&K'S CRITICISMS OF HARPOLE *ET AL.* (2016)

1. D&K stated that 'while experimental demonstration of these patterns does indicate a causal relationship between resource addition and species loss (or compositional divergence), it does not tell us anything about the mechanisms underlying these patterns'. We completely agree and we stated this: 'Stronger tests of the role of multiple resource competition for structuring species coexistence require physiological studies quantifying species-specific functional traits and trade-offs, and testing whether species respond to resource treatments similarly in different environments. Deeper mechanistic insight can also be gained by asking how resource-dependent diversity patterns and mechanisms change across scales (for example, from local to regional) in response to global change drivers such as nutrient pollution. Our results point to, but do not distinguish among, the presumed resource competition mechanisms that underlie the resource dimension hypothesis' (Harpole *et al.* 2016). While we manipulated the number of added nutrients and showed that the number of nutrients drove changes in species diversity and composition in multiple ways that are consistent with the niche dimension hypotheses, a deeper level mechanistic explanation is clearly a needed future research topic, which we pointed to (Harpole *et al.* 2016).
2. D&K argued that the 'concept of discrete 'number' of limiting resources is too simplistic and should be replaced by more realistic concepts of co-limitation by multiple essential elements'. We agree that the essence of Hutchinson's (1957) prediction is simplistic – it was a geometric-based concept to make a simple but elegant argument (Hutchinson 1957). Nevertheless, this represents a 60-year-old prediction, which has only been tested and supported by a handful of studies in the past decade. Our motivation was to test the generality of this basic ecological prediction and explore the potential variability of multiple resource–diversity relationships across 45 grassland sites around the world. There is no question that Hutchinson's conceptual presentation of the niche dimension hypothesis needs greater development in terms of mechanism and realism. In fact, we have discussed extensively the realism of co-limiting

nutrients (Harpole *et al.* 2011; Fay *et al.* 2015), and we also stated that: ‘Estimating effective upper bounds on ecologically relevant resource dimensionality will depend on the degree to which multiple limiting factors covary, how they change in time and space, and how multiple limiting factors interact with each other in promoting coexistence’ (Harpole *et al.* 2016).

3. D&K argued that because sites (approximately one-third of 45 sites) where community biomass did not increase with added nutrients, nutrients were therefore not limiting and could not affect diversity. But they missed the logic and the point we made that although community biomass is the standard response variable for assessing nutrient limitation, multiple processes, from individual physiology to ecosystem level, can be limited by multiple nutrients, and, importantly, *that different processes can be limited by different nutrients* (Harpole *et al.* 2016; and discussed extensively in Harpole *et al.* 2011). We also pointed to multiple alternative mechanisms whereby changes in nutrient availability might negatively affect diversity indirectly: e.g. changes in other limiting factors including light, soil water and herbivory.
4. D&K criticise our experimental design for only adding soil nutrients, and that because ‘light supplementation was kept constant’ (because it was not directly manipulated), the number and the type of resource limitation was confounded. Expressed more precisely, what we said previously was: ‘Environmental change can therefore reduce the niche dimension of particular ecological communities through decreases in the number or heterogeneity of limiting resources or through changes in the identity and stoichiometry of limiting resources’ (Harpole & Tilman 2007). In other words, there are at least four interrelated mechanisms underlying the niche dimension hypothesis. As we also highlighted and have explored elsewhere (Cardinale *et al.* 2009), the total amount of resources and their ratios were also not experimentally independent, but these components are not exclusive and all are integral to the niche dimension hypothesis. We agree with D&K that these issues and others that we discussed (such as nutrient fertilisers being made of multielement salts and that individual elements are often available in different molecular forms) make quantification of effective dimensionality challenging. Our purpose was to test for the generality of evidence that would be consistent with multidimensional resource niches, within the constraints of a globally distributed factorial experiment that necessarily traded off the experimental design parameters of number of sites, replication within sites, treatment factor number and levels, and feasibility in terms of cost and sampling effort (Borer *et al.* 2014a). There is no question that there remain numerous questions and mechanisms to explore and we stand by our conclusion: ‘Our results point to the importance of understanding dimensionality in ecological systems that are undergoing

diversity loss in response to multiple global change factors’.

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

ULTIMATE VS. PROXIMATE CAUSES

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

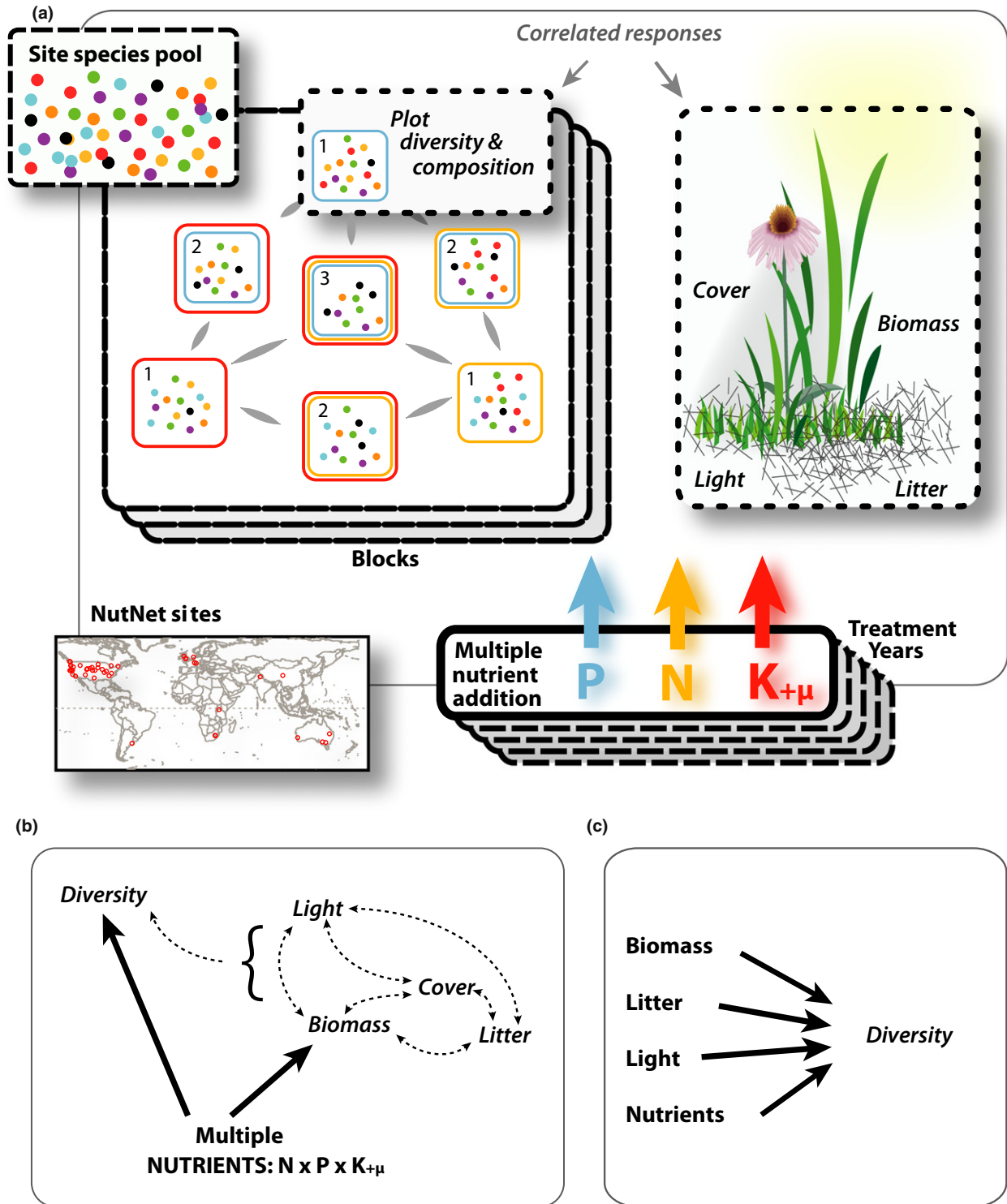


Fig. 1. (a) Illustration of our experimental design at each of the 45 grassland sites in this study (map). We applied factorial combinations of P, N and K plus micronutrients (μ) – the treatments – to plots as indicated by the blue, yellow and red boxes around each plot. Species are indicated by coloured 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 labelled 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 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) DeMalach & Kadmon (2017) tested the relative effects of live and dead biomass, light and nutrients as independent and direct drivers of diversity.

D&K therefore misapplied the multiple regression model that we originally presented as a heuristic illustration of the existing paradigm of diversity loss resulting from nutrient addition. In other words, Harpole *et al.* (2016) used that linear model simply to show that residual variation in plant diversity could still be explained by the number of added resources, after controlling for variation in the traditional or paradigmatic explanatory variables (e.g. live and dead biomass, and light) (Harpole *et al.* 2016). We used that model to ask the question, is there support for including niche dimensionality as a mechanism that might act independent of, and in addition to, the standard biomass-related mechanisms (Fig. 1b)? The model is technically incorrect because live and dead biomass and light are dependent variables and correlated, violating assumptions of linear regression, but we used the model as an 'added variable' test that provided just one of a number of lines of evidence that we used to support our conclusions. However, D&K next used the standardised multiple regression coefficients from that model to conclude that light was the 'main factor explaining diversity loss' and that the actual experimental treatment factors – multiple added nutrients – were unimportant and that therefore there was 'no support for the niche dimension hypothesis' (DeMalach & Kadmon 2017). They further suggested that the effects of nutrients were exaggerated because they were 'measured without variance' – a misunderstanding of the design because they were factor level treatments (Oehlert 2010). To highlight the logical and conceptual problems with their approach, we examined their methods further. What D&K omitted from the presentation of their analysis were the other variables in their model: the number of years of treatment, the site species pool and total plant species cover, all important aspects of the experiment and our questions. The standardised coefficients for these omitted variables show species pool sizes and the number of years of treatment to be much larger than that for light (Fig. 2a). By selecting only the 'main' variable having the largest coefficient, as D&K advocate, light as an explanation would be rejected. But, this would be the wrong conclusion and for the wrong reason.

Is light important? Yes, we agree completely with D&K and we showed that it was: 'We found that increasing the number of added resources increased live biomass. . . , and decreased the proportion of photosynthetically active radiation (PAR) transmitted through the canopy to the ground surface' (Harpole *et al.* 2016, p. 94). But changes in light depletion are just part of the multivariate suite of correlated responses that include live and dead biomass, total cover and species composition. Also potentially important are changes to variables we were not able to measure, e.g. physiology, allocation and traits; soil moisture, air temperature and humidity; herbivory, pathogens and mutualists; spatial heterogeneity and temporal changes in community dynamics; and ecosystem processes. However, we can still ask what is the relationship between light depletion and diversity if we properly account for added nutrients as the

independent variables, years of treatment and species pools as *covariates*, and diversity, live and biomass, cover and light as the set of correlated *response* variables (Fig. 1)? Here, correlations are the more reasonable way to describe the relationships among this last set of variables because causality can go both ways.

To explore the relationships between diversity and live and dead biomass (log-transformed), cover, and light (the *responses*), we quantified, for each, the residuals after controlling for the independent variables – both the effects of factorial addition of N, P and K + μ (the *treatments*), and species pool size and number of treatment years (the *covariates*), and the random variation associated with blocking factors (Fig. 1). After accounting for these effects, most response (i.e. *dependent*) variables remained significantly correlated with each other (Fig. 2b). Together, the independent variables explained 52% of variation in diversity. The remaining (*residual*) variation in diversity was positively and significantly correlated with light, but with an r^2 of only 0.017 (Fig. 2b, $r = 0.13$). The bottom line is that multiple nutrient addition and larger scale diversity are the main explanatory variables for the response of diversity in this experimental study. Then, what might be the role of light, as a response and a potential proximate causal factor, within a niche dimensional framework?

CONCEPTUAL ILLUSTRATION OF THE MULTIDIMENSIONAL NICHE

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

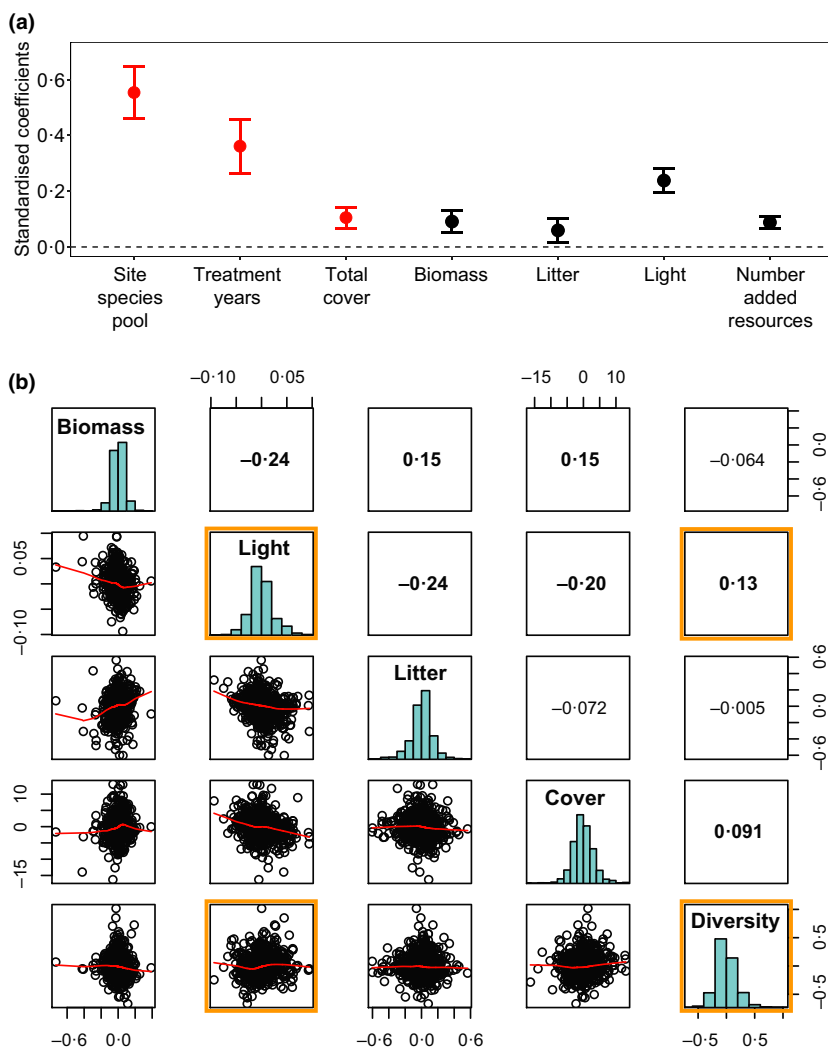


Fig. 2. (a) Recreated plot from D&K showing the relative sizes of the standardised coefficients of the response variables live and dead biomass, photosynthetically active radiation (light) and the independent variables the number of added resources (means \pm SE in black). The variables in the model 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 \pm SE 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.

there should be fewer trade-off possibilities for *those species adapted to and coexisting under the original conditions*; competition occurs for limiting, not non-limiting factors (Harpole & Tilman 2007).

More precisely, this *niche dimension* hypothesis predicts that ‘Environmental change can therefore reduce the niche dimension of particular ecological communities through decreases in the number or heterogeneity of limiting resources or through changes in the identity and stoichiometry of limiting resources’ (Fig. 3; Harpole & Tilman 2007, p. 791). Thus, addition of limiting resources should lead to loss of species diversity generally, but this effect will depend critically on how the ‘balance’ or stoichiometry of the limiting resources (including light and many other factors) changes (Cardinale *et al.* 2009; Lewandowska *et al.* 2016). In some cases, we might expect addition of particular combinations of resources to restore a balanced supply of resources that promotes coexistence, which is the mechanism that Hautier, Niklaus & Hector (2009) found when they experimentally added light back to the understorey of fertilised communities, refuting the interpretation of DeMalach & Kadmon (2017). The consequences of

altered resource supply also depend on the relationships between the pool of species present, the multivariate set of traits and trade-offs they represent, and how these map onto multivariate resource supply clouds (Fig. 3). However, because there are practical limits to the number of factors that can be tested in one experiment, we focused on combinations of three nutrient resource treatments. We acknowledged although that other factors are important in structuring diversity and these can interact with resources, such as micronutrients and toxins, soil properties including pH, pathogens and specialised herbivores. Given that changes in nutrient supply can drive complex relationships among environmental factors, our observation that light limitation is an important but not a necessary driver of diversity loss should not be controversial.

By promoting light asymmetry as their main explanation for the negative effects of nutrients on diversity, D&K ignore evidence showing that the effects of light depletion are not always negative. Shading can have positive effects on diversity, including when facilitating plant recruitment in moisture-stressed environments (e.g. Carson & Pickett 1990; Dickson & Foster 2011; Richardson *et al.* 2012). We

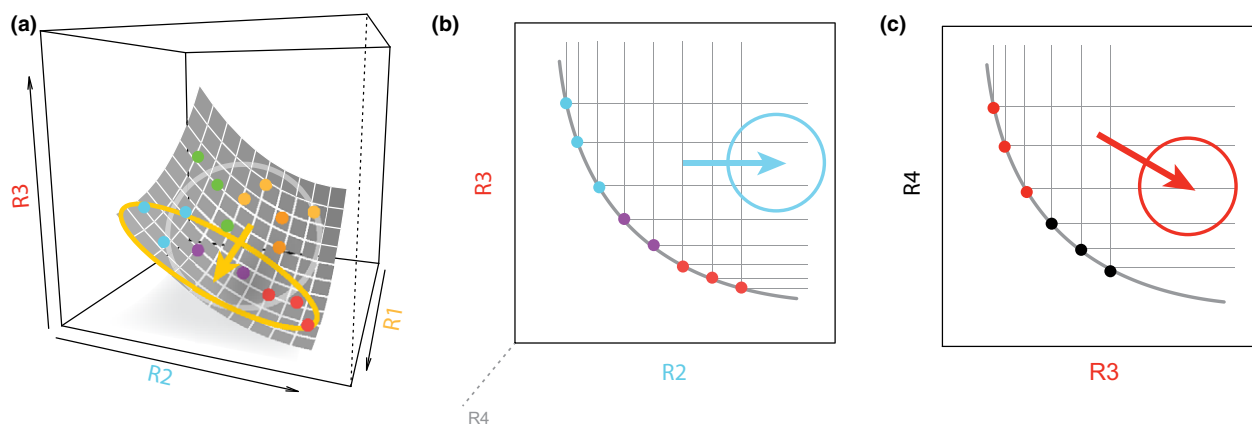


Fig. 3. Resource addition can reduce the niche dimension of particular ecological communities by decreasing the (i) number, (ii) stoichiometry, (iii) identity or (iv) heterogeneity of limiting resources (Harpole & Tilman 2007). (a) Species competing through trade-offs in their minimum requirements for three resources (R1, R2 and R3). The grey plane represents the trade-off 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 favouring 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).

showed elsewhere how nutrient addition negatively affects soil moisture (Harpole, Potts & Suding 2007), and water and nitrogen generally co-limit plant communities across a wide range of precipitation (Hooper & Johnson 1999; Eskelinen & Harrison 2015). Therefore, addition of multiple nutrient resources need not necessarily shift competition to above-ground light but can shift the identity of limiting resources to an alternative below-ground resource such as water (for example, see Simkin *et al.* 2016). Changes in resources can also change trophic relationships, which are often as or more important than limiting resources (Borer *et al.* 2014b). Nutrient addition can change rates of herbivory by changing the quantity and quality of plant tissue and drive changes in the relative abundance of species that differ in their susceptibility, defences and responses to different consumers; herbivores, in turn, can contribute to the maintenance of diversity by stabilising plant community evenness (Mortensen *et al.* 2017). And, we must remember that these are grassland ecosystems that are strongly defined by grazers and water availability (Frank, McNaughton & Tracy 1998).

SUMMARY

Our findings highlighted that multiple nutrient limitations can structure plant diversity and composition independently of changes in biomass and light. Approximately one-third of our sites showed no significant increase in biomass with greater number of added nutrients, yet these sites still lost diversity when nutrients were added and composition changed in ways consistent with species' trade-offs for different limiting resources (Harpole *et al.* 2016). The important message was that while light

limitation can be an important contributor to diversity loss, it is not the only or even a necessary mechanism. But the essential issue here is whether attempting to identify a single 'main' factor is adequate or insightful to explain complex ecological phenomena; we contend it is not. D&K's misrepresentation of causality only distracts from progress towards understanding the multivariate drivers of diversity. Furthermore, the question that is left open by D&K is that even if fertilised plots lose diversity mainly due to light competition, this says nothing about how diversity was maintained in the unfertilised plots that were limited by multiple nutrients and presumably not limited by light. The light asymmetry hypothesis does not help us understand the maintenance of diversity in plant communities where nutrients have not been added. In addition, because we experimentally manipulated nutrients, not light, a direct light \times nutrient manipulation experiment would be necessary for a true comparison of these mechanisms and their interactions. We reiterate our call to work towards multivariate and mechanistic experiments and models for plant diversity that integrate the multiple mechanisms that have been demonstrated in natural systems (Grace *et al.* 2016). There is much more to plant communities than the shadows on the lawn.

Authors' contributions

W.S.H. analysed the data and wrote the paper with contributions and input from all authors.

Data accessibility

All data and supporting information used in this manuscript were presented in Harpole *et al.* (2016), the subject of this comment article.

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