Community composition mediates grassland biomass responses to nutrient addition and rainfall variation.

Siddharth Bharath, Elizabeth T. Borer, Nutnet Coauthors… Eric W. Seabloom

Key Questions:
In grassland plant communities, how does community composition mediate the responses of biomass to experimental nutrient addition and natural rainfall variation.
1) How is temporal turnover in species composition related to the responsiveness of biomass to precipitation change at a site?
2) Do species show trade-offs in their responses to nutrient addition and to rainfall variation?

Key Reading:
Eskelinen, A. and Harrison, S.P., 2015. Resource colimitation governs plant community responses to altered precipitation. *Proceedings of the National Academy of Sciences*, *112*(42), pp.13009-13014.

Bonus Reading (for similarity in methodology):
Lind, E.M., Borer, E., Seabloom, E., Adler, P., Bakker, J.D., Blumenthal, D.M., Crawley, M., Davies, K., Firn, J., Gruner, D.S. and Stanley Harpole, W., 2013. Life-history constraints in grassland plant species: A growth-defence trade-off is the norm. *Ecology letters*, *16*(4), pp.513-521.

Feedback requested: Please answer one of these questions -
1. Do you have any thoughts on the conceptual framing of Figure 1?
OR
2. What is the most exciting hook or take-home message from this paper?

Please fill the coauthorship opt-in table online after reading the paper, if you want to opt in.

Introduction
1. Grassland biomass varies a great deal over time, largely driven by interannual variation in precipitation. Water can be viewed as one of multiple resources limiting biomass production, thus part of the temporal variation in biomass is due to the sensitivity of the ecosystem to variation in water. Alleviating nutrient limitation should lead to biomass and species abundances being more sensitive to changes in water availability.

2. Community composition can mediate the effects of resource changes on biomass production and stability. The relationship between compositional sensitivity and biomass sensitivity to precipitation is different in different places (Hallett et. al 2014), and is likely to be changed by nutrient addition.

3. There are 4 possible scenarios of how biomass sensitivity is related to community sensitivity (Figure 1a). First,it is possible for biomass to vary strongly with precipitation, but the same set of species persist through high and low rainfall years (quadrant A, Figure 1a). Secondly, there can be a strong coupling of community composition and biomass production – production in high rainfall years is higher and driven by a set of species different from the low production in low rainfall years (quadrant B, Figure 1a). Thirdly, biomass production can be stabilized by turnover that selects for species which grow well in different conditions (quadrant D, Figure 1a). Finally, it is possible for both community composition and biomass to be unresponsive to precipitation change (quadrant C, Figure 1a). In each of these scenarios, nutrient addition can have different effects on the sensitivity of biomass and composition to precipitation.

4. Multiple resource limitation predicts that adding nutrients should increases biomass sensitivity to rainfall (Huxman et al. 2004, Bharath et al. 2020), which could happen through reduced asynchrony among species (Hautier et al. 2014) or increased sensitivity of existing species to rainfall change. Reich (2014) proposed that plant traits for acquisition and usage of carbon, water and nutrients are physiologically correlated such that plants fall along a fast-slow economic spectrum of life history strategies. If that is the case within a community, species responses to nutrient addition and precipitation variation should be positively correlated (fast-slow case, Figure 1b) i.e. species that increase in abundance under fertilization also increase with water availability, thus making community biomass more sensitive to rainfall variation. Alternatively, if there is a trade-off among species between performance at high nutrient availability and high water availability, then there should be a negative correlation between species responses to nutrients and water (tradeoff case, Figure 1b). In these two cases of linear correlation, addition of nutrients selects for a subset of plant species with a smaller range of water responses than the original community – which could increase (for the fast-slow case) or decrease (for the tradeoff case) biomass sensitivity to rainfall. However, if there is no linear correlation between species responses to water and nutrients, then nutrient addition should not strongly impact biomass sensitivity to rainfall (High dimensional case, Figure 1b).

We use data from a distributed long term (5-11 year) fertilization experiment conducted at 34 grassland sites around the world, to answer three questions –
1) How does biomass sensitivity to water availability relate to community composition sensitivity to water availability?
2) How does nutrient addition shift the aggregate community response to varying water availability?
3) How do abundance of individual species respond to changes in nutrient availability (as experimental addition) and water availability (as variation over time)?

Methods (outline)

<u>NutNet experimental protocol</u>

<u>Weather data</u>

We measured annual water availability at a site by calculating the Standardized Precipitation Evapotranspiration Index (SPEI) for the duration of the growing season. This a normalized index that expresses current year water deficit (precipitation – evapotranspiration) relative to the history of rainfall variation at the site. Values of SPEI follow the distribution of a standard normal distribution (mean = 0, standard deviation = 1), and make relative water availability comparable across sites.
Of 40 sites with 5+ years of data in NutNet, 34 sites experienced both a dry year that had an SPEI of at least -0.9, and at least 2 units of variation in SPEI during the course of the experiment. All further analysis was only done for those 34 sites, as we considered them to have sufficient rainfall variation to be able to measure the effects of water availability on plant communities..

<u>Data Analysis for Question 1 and 2</u>

We measured sensitivity of community composition to interannual water variation by calculating the fraction of variance in community composition that is explained by SPEI, based on a PERMANOVA (fit using RRPP, Collyer and Adams 2018). We measured sensitivity of biomass to water variation by calculating the correlation coefficient between biomass and SPEI (Supplementary Figure 1). We calculated both of these separately in control and nutrient added plots, and then estimate the effect of nutrient addition on community sensitivity and biomass sensitivity.

<u>Data Analysis for Question 3</u>

We subset our species cover data to only include vascular plant species that were observed in 20% or more of all samples within a site, and observed in more than one year at a site.
We estimated individual species responses to experimental nutrient addition and natural rainfall variation through linear models (PERMANOVA) fit using RRPP (Collyer and Adams 2018). We plotted the relationship between the linear response coefficients of nutrients and water among species at a site. This enabled us to classify sites in one of 5 categories – Fast-Slow, Trade-off, High Dimensional, Nutrient-Controlled, or Water Controlled – based on the calculated Pearson correlation between response coefficients of nutrients and water, and the significance of nutrients or water as drivers of community composition in the PERMANOVA.

Results

1) 1) How does biomass sensitivity to water availability relate to community composition sensitivity to water availability?

- Among the 34 sites with sufficient precipitation variation during the experiment, we find 10 sites where biomass shows a negative or zero correlation with water availability (see Figure S1, Table S2), suggesting that growth in those sites is not limited by water, or more water can be a stressor for growth.
- In the remaining 24 sites, we find plant communities distributed across all quadrants of the possible relationships between biomass and community sensitivity (Figure 2a), except for the quadrant of high community sensitivity but low biomass sensitivity (Quadrant D in Figure 1a).

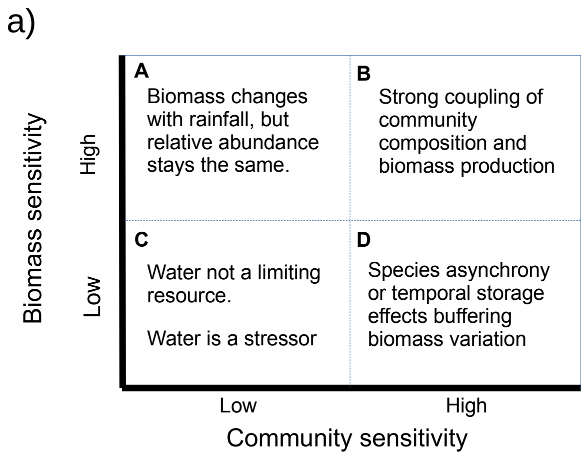
2) How does nutrient addition shift the aggregate community response to varying water availability?

- Nutrient addition increases biomass sensitivity to precipitation at 13 (54%) sites, and increases community sensitivity to water availability at 17 (71%) out of 24 sites (Figure 2). However, we also see sites with large decreases in biomass and/or community sensitivity to water availability (Table S2, Figure S3).
- Nutrient addition shifts more sites into the region of high community sensitivity but low biomass sensitivity (Quadrant D of Figure 1a).

3) How do abundance of individual species respond to changes in nutrient availability (as experimental addition) and water availability (as variation over time)?

- Our classification of sites based on correlation of nutrient response and water response in the community resulted in the following distribution of the 34 sites in the different categories (See Figure 3 and Figure S2) –
    - Fast-slow (1),
    - Tradeoff (7),
    - High Dimensional (14),
    - Nutrient Controlled (11)
    - Water controlled (1)
- The sites that shift to Quadrant D under nutrient addition are all sites that are classified as having High Dimensional community structure with respect to water and nutrients. (See Figure S3)
- Sites that are classified as Nutrient Controlled based on species responses are all in Quadrant C, showing low biomass or community sensitivity response to rainfall, as should be expected.

Figure 1: a) Different scenarios of how biomass sensitivity to rainfall can relate to community compositional sensitivity to rainfall, and the mechanisms that correspond to each scenario.
b) Different scenarios of the distribution of species in a community with regards to individual species responses to experimental nutrient addition and natural rainfall variation.



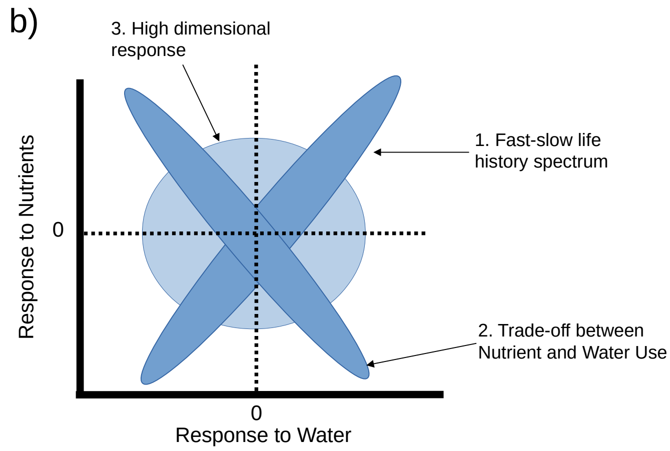


Figure 2: The relationship between biomass and community sensitivity to water availability at 24 sites in a) Control plots and b) NPK fertilized plots. Each point denotes a site. Biomass sensitivity is the correlation coefficient between scaled biomass and SPEI, community sensitivity is the fraction of variance in community composition that is explained by SPEI.

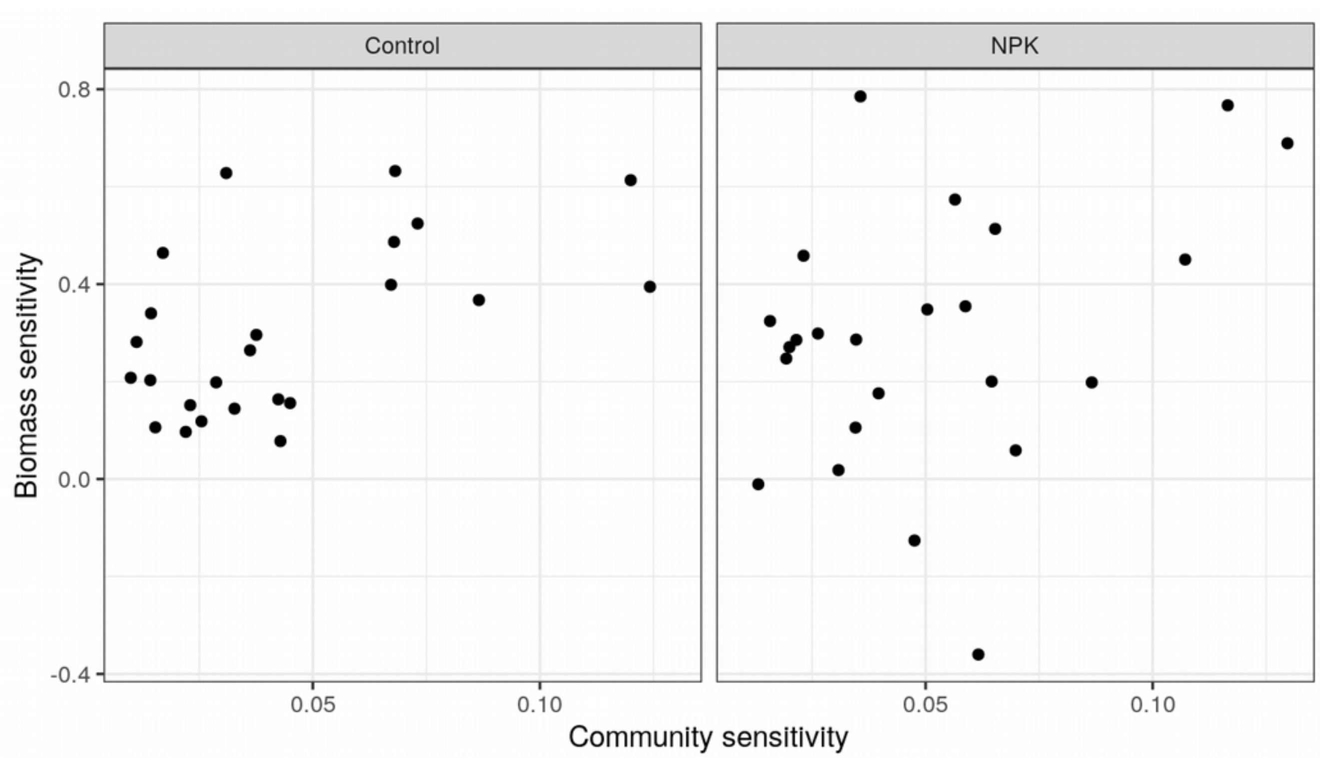
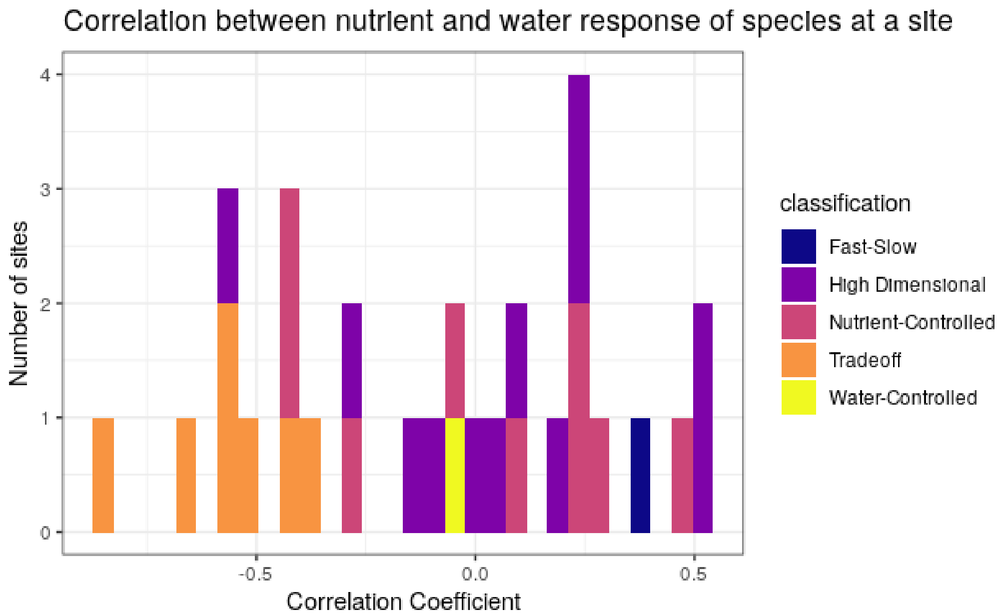


Figure 3: Site scale correlations between species responses to nutrients and species responses to rainfall. This is a histogram of the Pearson correlation coefficient between nutrient and water responses of all species in the community of a site, for 34 grassland sites. Communities are classified as having positive correlation (Fast-Slow), negative correlation (Tradeoff), or no correlation (High Dimensional, Nutrient Controlled or Water Controlled) between the two responses.



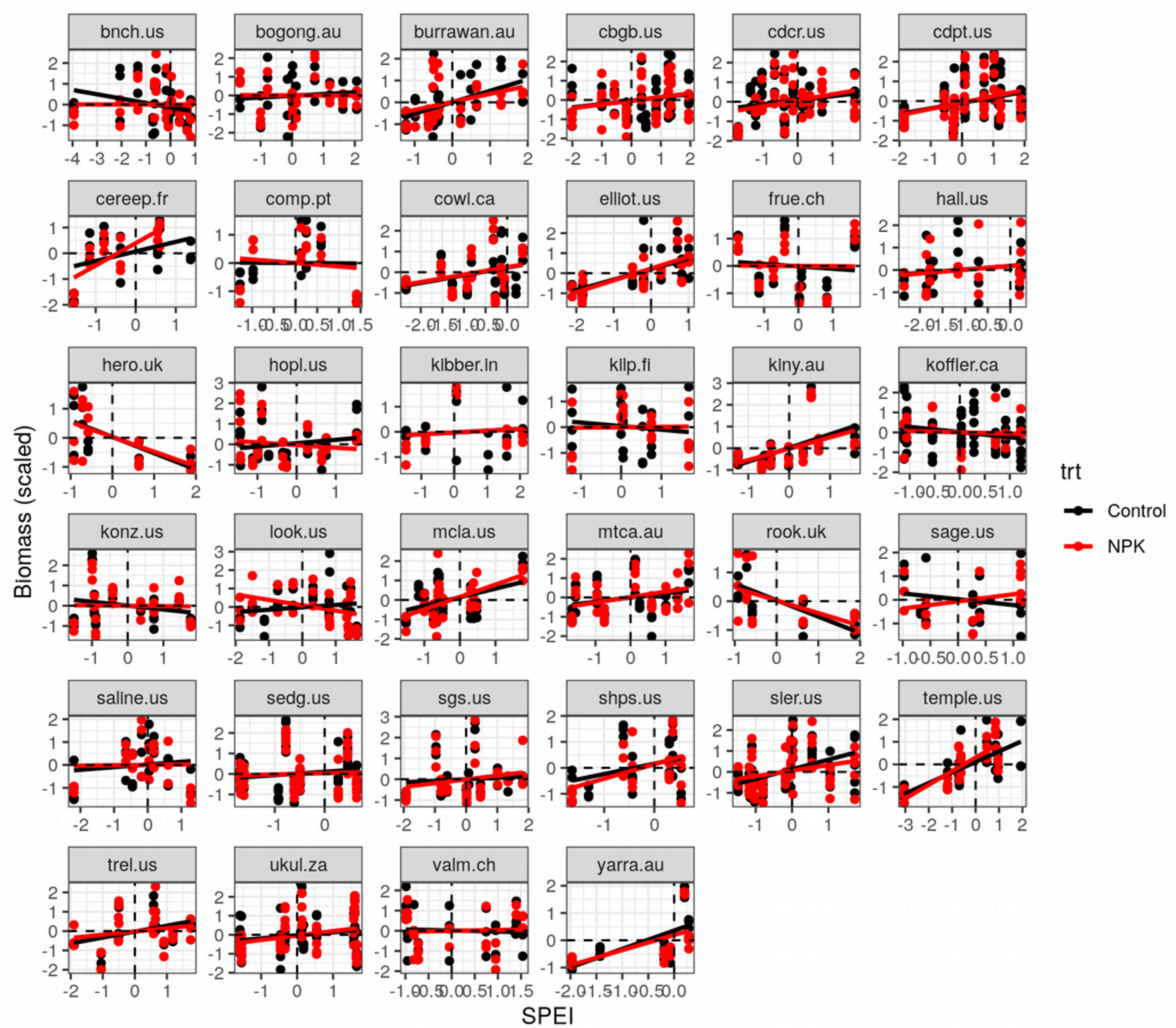
Supplementary Table S1

Sites used in this analysis along with duration of weather, biomass and cover data at each site. The Aridity Index is the ratio of mean precipitation and mean evapotranspiration in the growing season. Maximum and Minimum values of SPEI experienced during the experiment duration at each site are also shown.

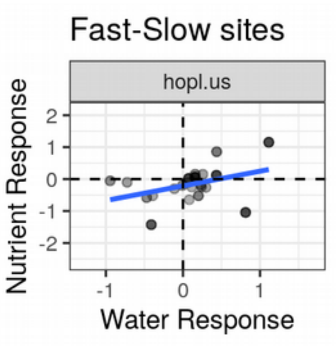
Site Code	Weather duration (yrs)	Biomass duration (yrs)	Cover duration (yrs)	Aridity Index	Min SPEI	Max SPEI
bnch.us	52	12	12	0.63	-3.94	0.82
bogong.au	24	11	11	1.44	-1.66	2.06
burrawan.au	51	12	12	0.4	-1.23	1.87
cbgb.us	41	10	10	0.91	-2.01	1.94
cdcr.us	51	12	12	0.73	-1.71	1.64
cdpt.us	22	12	12	0.43	-1.85	1.88
cereep.fr	38	7	7	0.68	-1.54	0.6
comp.pt	10	6	7	1.08	-1.28	1.41
cowi.ca	43	12	12	0.38	-2.34	0.36
elliot.us	51	10	11	0.54	-2.11	1.01
frue.ch	13	8	8	2.03	-1.76	1.64
hall.us	42	8	8	0.74	-2.35	0.23
hero.uk	32	5	7	0.59	-0.92	1.87
hopl.us	17	12	12	3.11	-1.45	1.54
kibber.in	38	6	8	0.64	-1.47	2.08
kilp.fi	40	6	6	1.12	-1.22	1.68
kiny.au	47	10	10	0.49	-1.25	1.6
koffler.ca	13	8	8	0.59	-1.11	1.22
konz.us	21	10	11	0.61	-1.5	1.76
look.us	24	12	12	1.57	-1.87	1.63
mcla.us	33	12	12	1.91	-1.51	1.77
mtca.au	50	10	10	0.22	-1.67	1.66
rook.uk	32	5	7	0.59	-0.92	1.87
sage.us	40	7	7	0.25	-0.98	1.14
saline.us	51	8	10	0.47	-2.19	1.28
sedg.us	48	10	10	0.39	-1.7	0.64
sgs.us	15	12	12	0.25	-1.93	1.81
shps.us	52	7	10	0.2	-1.64	0.69
sier.us	50	12	12	2.32	-1.49	1.73
temple.us	49	9	9	0.53	-3.05	0.96
trel.us	51	9	10	0.69	-1.9	1.74
ukul.za	39	10	10	0.66	-1.59	1.66
valm.ch	16	10	10	0.88	-0.99	1.54
yarra.au	24	6	6	0.48	-1.97	0.28

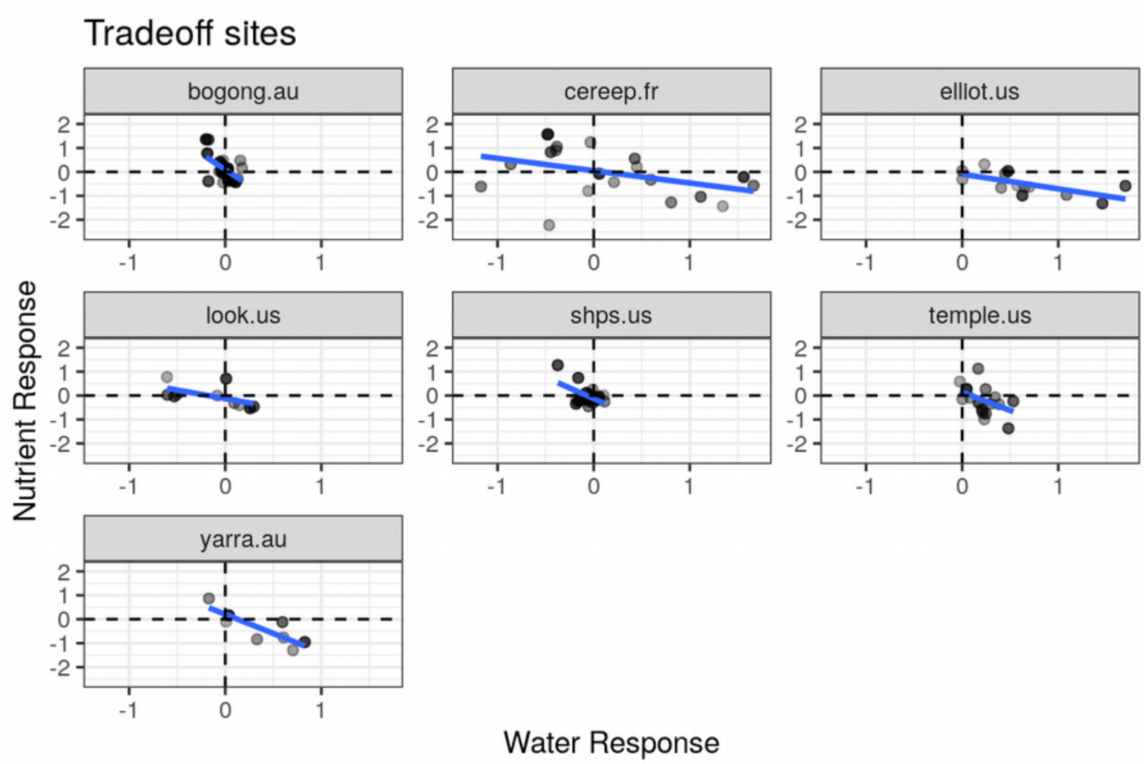
Supplementary Figure S1

Measurement of biomass sensitivity to water availability for control and NPK plots at each of 34 sites in this study. Biomass values for each treatment are scaled and centered to have a mean of 0 and standard deviation of 1. Control plots are in black, nutrient added plots are in red.



Supplementary Figure S2
Distribution of response to experimentally added nutrients and naturally varying water availability among species at a site. Sites are grouped as per the classification in the text. Each species at a site is represented by a point, with darkness of the point indicating the occupancy of the species. For sites with significant linear correlation between the responses, a best fit linear regression line is shown. For all other sites the distribution of species responses is shown by a 90% ellipse. Ranges of x and y axes are identical across all graphs.





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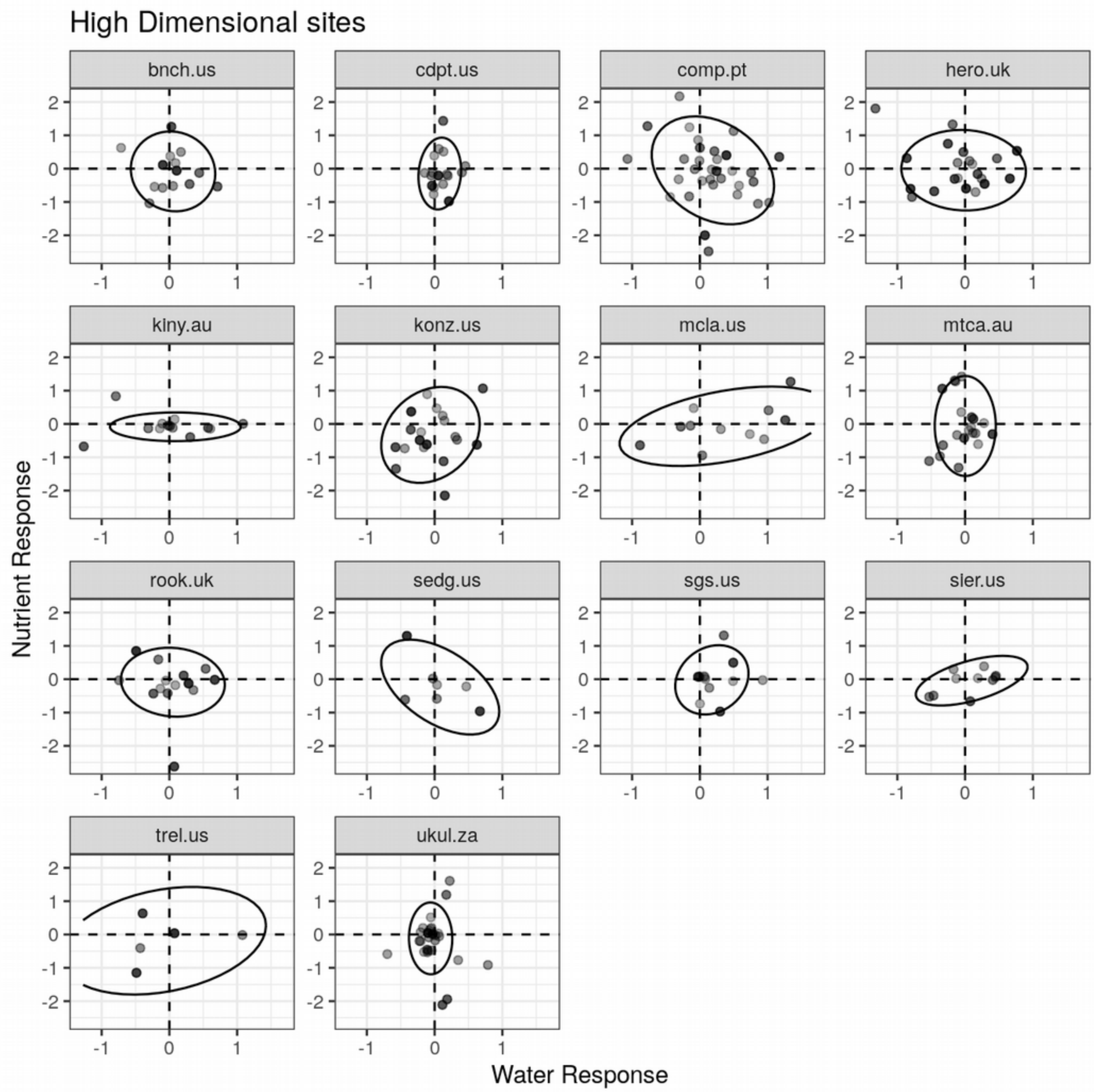

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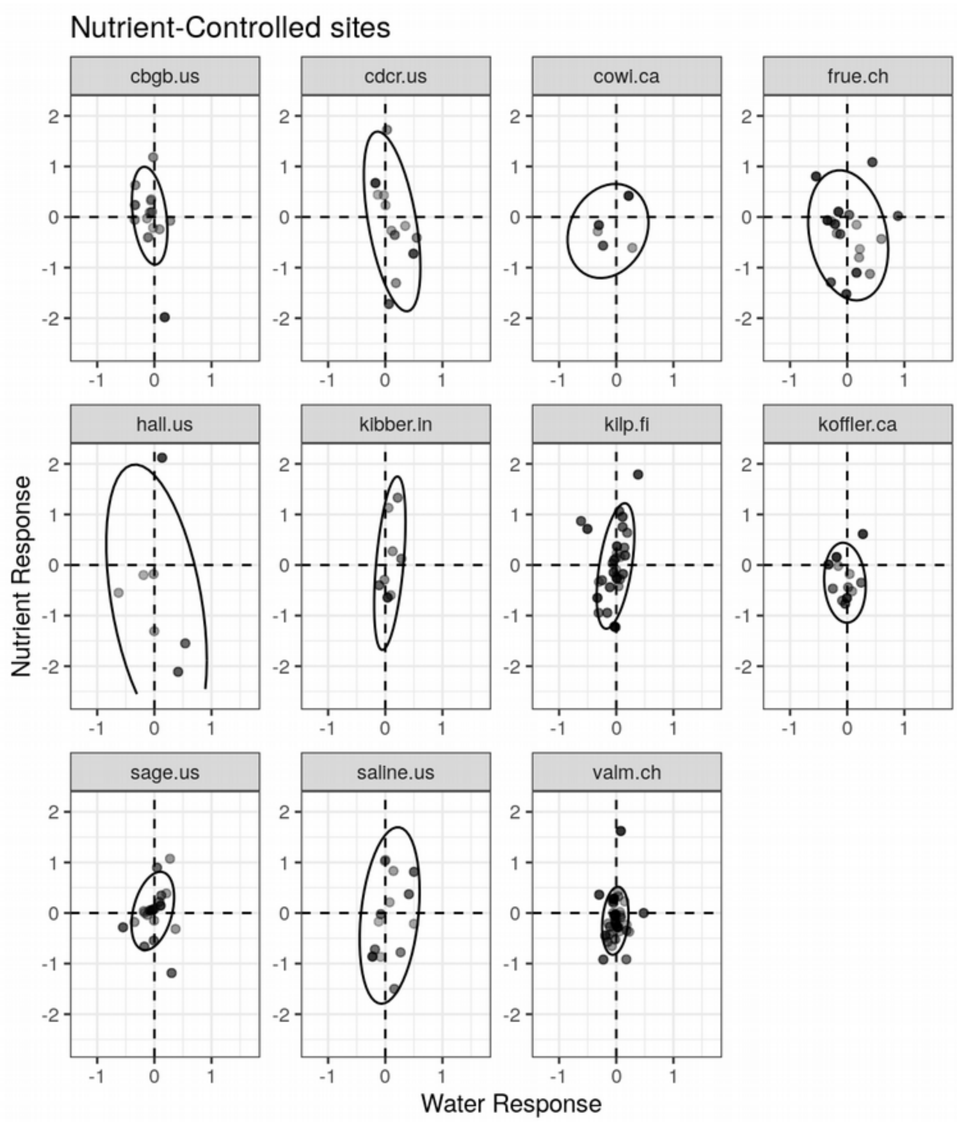

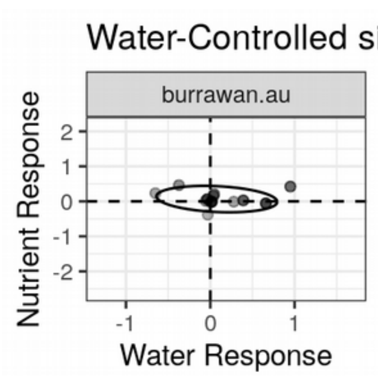

Supplementary Table S2

Estimated parameters for 34 sites in relation to the core questions of this paper. Sites marked with * are those with zero or negative biomass sensitivity to water availability, and are not included in Figure 2. Biomass sensitivity is the correlation coefficient between scaled biomass and SPEI, community sensitivity is the fraction of variance in community composition that is explained by SPEI.

Site Code	**Community Sensitivity**	**Biomass Sensitivity**	**NPK effect on Community Sensitivity**	**NPK effect on Biomass Sensitivity**	**Community Classification**
bnch.us *	0.04	-0.28	0.02	0.28	High Dimensional
bogong.au	0.02	0.11	0	-0.12	Tradeoff
burrawan.au	0.07	0.49	-0.01	-0.13	Water-Controlled
cbgb.us	0.01	0.21	0.01	0.04	Nutrient-Controlled
cdcr.us	0.01	0.2	0.02	0.08	Nutrient-Controlled
cdpt.us	0.01	0.28	0	0.04	High Dimensional
cereep.fr	0.12	0.39	-0.01	0.37	Tradeoff
comp.pt *	0.11	-0.01	-0.02	-0.11	High Dimensional
cowi.ca	0.04	0.3	-0.02	-0.01	Nutrient-Controlled
elliot.us	0.12	0.61	0.01	0.08	Tradeoff
frue.ch *	0.05	-0.09	-0.01	0.08	Nutrient-Controlled
hall.us	0.02	0.15	0.02	0.02	Nutrient-Controlled
hero.uk *	0.11	-0.66	-0.06	0.06	High Dimensional
hopl.us	0.04	0.16	0	-0.28	Fast-Slow
kibber.in	0.02	0.1	0.01	0.01	Nutrient-Controlled
kilp.fi *	0.04	-0.13	0.01	0.15	Nutrient-Controlled
kiny.au	0.07	0.52	0.03	-0.07	High Dimensional
koffler.ca *	0.01	-0.23	0.04	0.17	Nutrient-Controlled
konz.us *	0.07	-0.22	-0.03	0.19	High Dimensional
look.us	0.04	0.16	0.02	-0.52	Tradeoff
mcla.us	0.07	0.4	-0.01	0.17	High Dimensional
mtca.au	0.04	0.26	0.01	0.08	High Dimensional
rook.uk *	0.07	-0.67	0	0.15	High Dimensional
sage.us *	0.02	-0.21	0	0.47	Nutrient-Controlled
saline.us	0.03	0.12	0.01	-0.1	Nutrient-Controlled
sedg.us	0.03	0.14	0.04	-0.09	High Dimensional
sgs.us	0.04	0.08	0.02	0.12	High Dimensional
shps.us	0.01	0.34	0.01	0.12	Tradeoff
sier.us	0.02	0.46	0	-0.19	High Dimensional
temple.us	0.03	0.63	0	0.16	Tradeoff
trel.us	0.09	0.37	0	-0.17	High Dimensional
ukul.za	0.03	0.2	0	0.1	High Dimensional
valm.ch *	0.01	-0.06	0.01	0.1	Nutrient-Controlled
yarra.au	0.07	0.63	0	-0.12	Tradeoff

Supplementary Figure S3
Effect of nutrients on biomass and community sensitivity to precipitation. Arrows show the change in sensitivity from control to nutrient added plots (tail to arrowhead). The different panes correspond to classification of the different communities based on the correlation between species responses to nutrients and species responses to water availability. Sites in blue are the 24 sites which are limited by water, whereas sites in red are the 10 sites with zero or negative correlation of biomass with water availability.