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Species origin affects the rate of response to interannual growing season precipitation and nutrient addition in four Australian native grasslands

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Abstract

Questions: Predicted increases in temperature and changes to precipitation are expected to alter the amount of plant available nutrients, in turn, altering rates of primary production and exotic plant invasions. However, it remains unclear whether greater responses occur in wetter than average years, even in low fertility and low rainfall regions.

Location: Four Australian grasslands, including sites located in arid Western Australia, semi-arid Victoria, alpine Victoria and sub-tropical Queensland.

Methods: Using identical nutrient addition experiments, we use 6-yrs of biomass, cover and species richness data to examine how rates of biomass production and native and exotic cover and richness are affected by growing season precipitation (proportion of yearly GSP to long-term mean GSP) and nutrient (nitrogen, phosphorus, potassium, and micronutrients) addition.

Results: Rates of grassland productivity strongly increased with increasing GSP. GSP increased rates of native cover but not native or exotic richness, nor rates of exotic cover change. We detected no significant NPK effect on rates of grassland productivity, exotic cover or exotic richness change. By contrast, NPK addition decreased rates of native cover change and fertilized plots had significantly fewer native species. We did not detect a significant interaction between NPK and GSP.

Conclusions: Grassland productivity was more strongly predicted by variation in growing season precipitation than by nutrient addition, suggesting it will vary with future changes in rainfall. Response to nutrients, however, depend on species origin, suggesting that increasing soil nutrient availability due to anthropogenic activities is likely to lead to negative effects on native species richness and cover.

Keywords: Bayesian hierarchical models; Precipitation; Primary productivity; Nutrient Network; Rate change; Species richness

Introduction

At global and regional scales, primary productivity is highly correlated with total annual precipitation in natural grasslands (Sala et al. 1988; Bai et al. 2004; Yang et al. 2008). Interannual variation in precipitation also has been shown to affect primary productivity at local scales (Sala et al. 1988, 2012; Paruelo et al. 1999; Knapp et al. 1998, 2001; Swemmer et al. 2007). As such, there is general consensus that grassland productivity is sensitive to both the magnitude and timing of rainfall (Knapp et al. 2001; Sala et al. 2012). However, grassland productivity is also influenced by soil fertility in both dry (Hooper & Johnson 1999; Yahdjian et al. 2011) and wet conditions (Lee et al. 2010). In many grasslands, nutrient limitation can affect primary productivity, either singly or via co-limitation (Elser et al. 2007; Harpole et al. 2011; Fay et al. 2015), and have important consequences for species diversity (Harpole & Tilman 2007; Borer et al. 2014a). However, it remains unclear how both precipitation and soil fertility interact to affect rates of primary production in grasslands, and consequent changes in native and exotic species richness.

In Australia, a long history of weathering has led to nutrient-deficient soils that are quantitatively different from those of other continents (Specht & Specht 1999; Orians & Milewski 2007; Hopper 2009). The native flora is well-adapted to low nutrient availability (Dorrough & Scroggie 2008; Lambers et al. 2010; Laliberte et al. 2014), particularly P-limitation (Specht 1963). Hence, while many Australian soils are nutrient-limited for growth (Hayes et al. 2014), meaning that fertilizer addition is a typical practice in agriculture to enhance productivity of the exotic species used for pasture improvement (Leeper & Uren 1993), nutrient addition does not always lead to increased growth of native perennial species (e.g. Specht 1963; McIntyre & Lavorel 1994; Specht & Specht 1999; Dorrough & Scroggie 2008; Smallbone et al. 2008). While plant communities on soils with low nutrient availability have been shown to be highly responsive to nutrient additions elsewhere in the world (e.g. Going et al. 2009), such responses remain largely undocumented for Australian grasslands. Indeed, while Price & Morgan (2007) showed that three years of fertiliser addition increased primary productivity in temperate herb-rich woodlands, these effects were mostly because of increases in productivity of exotic species. Hence, sensitivity of Australian grassland productivity to nutrient addition remains unclear. Additionally, the magnitude of the nutrient addition effect in grasslands is likely to increase with increasing plant available water, i.e. nutrient addition interacts positively with growing season precipitation (Swemmer et al. 2007; Lee et al. 2010; Hall et al. 2001; Yahdjian et al. 2011; Prober & Wiehl 2012; Dwyer et al. 2015). Year-dependent effects on primary production are therefore likely to be particularly important in Australian grasslands because the El Niño–Southern Oscillation (ENSO) cycles cause large inter-annual variation in precipitation (Vines et al. 2004). Indeed, globally, rainfall in Australia is the most variable of any landmass (McMahon et al. 1992; van Etten 2009).

Australian grasslands are not well represented in global studies of rainfall - production (Sala et al. 2012) and, in many cases, Australian grasslands are at the lower end of the rainfall gradient studied by ecologists elsewhere (e.g. Lee et al. 2010). A robust assessment of the extent to which water and nutrient availability limit productivity in Australian grasslands under present climatic conditions is therefore needed. Here, we use a six year dataset from identical experimental nutrient additions conducted at four grassland sites in Australia to address three fundamental hypotheses: (1) nutrients and growing season precipitation limit *rates* of biomass production; (2) nutrients and growing season precipitation are co-limiting, which result in a positive interaction between their effects on rates of biomass production, and; (3) native and exotic species will respond in different ways to nutrient addition and growing season precipitation, reflecting their different evolutionary histories. To address these questions, we explicitly model experimental treatment (i.e. nutrient addition) and temporal covariates (i.e. GSP) on *rates* of biomass production, rates of exotic and native cover change, and their effects of native and exotic richness.

Methods

Study design

We use data collected for the Nutrient Network experiment (www.nutnet.org), a distributed, research cooperative dedicated to the study of productivity-diversity relationships in grasslands worldwide (Borer et al. 2014b). Sites in the network are dominated primarily by herbaceous vegetation, principally in the northern hemisphere. The standard design is a completely randomized block design with three blocks and 10 plots per block at each site. Nutrients are added as single-factor treatments or in factorial combinations. We use the control (unfertilized) plots and those receiving full fertilizer (NPK + micronutrients) that were fenced to exclude all vertebrate herbivores. In year 1, pre-treatment species composition and biomass were recorded. In year 2, and each year thereafter, NPK was added. Nutrient addition rates and sources were: 10 g N m^2 yr^{-1}, as time-released urea; 10 g P m^2 yr^{-1}, as triple superphosphate; 10 g K m^2 yr^{-1}, as potassium sulphate. Micronutrients were added once at the start of year 2 (100 g m^{-2}, comprising 6% Ca, 3% Mg, 12% S, 0.1% B, 1% Cu, 17% Fe, 2.5% Mn, 0.05% Mo and 1% Zn). Study plots had a perimeter of 5 x 5 m and were separated by 1 m walkways. A single 1 x 1 m subplot within each plot was permanently marked and sampled for species composition during the season of peak biomass by estimating the percent cover of all species rooted within the quadrat.

Annual live biomass was sampled at the peak of the growing season immediately adjacent to the permanent vegetation subplot. Vegetation was sampled destructively by clipping at ground level all aboveground biomass of individual plants rooted within two 0.1 m^2 (10 x 100 cm) strips per plot. For each year, biomass was sorted into live and dead material. Biomass was dried at 60 °C for 48 hrs and weighed to the nearest 0.01 g. We used the current year's aboveground live biomass as our estimate of annual above-ground productivity. Further details on study design can be found at Borer et al. (2014a, b).

We analyzed data from four Australian grassland sites in the Nutrient Network (established in 2007/08, through to 2013/14) that differed in their soil characteristics (pH, nitrogen, phosphorus), mean annual precipitation (MAP) and where inter-annual variation in growing season precipitation (GSP) is high (Table 1). All sites are variably dominated by grasses at peak biomass, the functional group most responsive to precipitation in the preceding months (Sala et al. 2012), though the sites differ in the relative abundances of native and exotic species. Our sites span a rainfall and temperature gradient (Table 1) and, relative to other grassland biomes, have low soil nutrients (particularly P; Fay et al. 2015) and higher rainfall variability than grasslands in the central United States (mean 27% coefficient of variation; Knapp et al. 1998). At three sites (Burrawan, Kinypanial, Mt Caroline), low soil water, not low temperature, determines the length of the growing season (i.e. 'empty bucket systems' *sensu* Knapp et al. 2006); at Bogong, the growing season coincides with the warmer, snow-free period. We therefore examine the effects of GSP on biomass production independent of total annual precipitation given strong seasonality in growth is evident at all sites.

To evaluate the relationship between inter-annual variation in live biomass production with nutrient addition (NPK) and the proportion of yearly GSP to long-term mean GSP, we examined peak live above-ground biomass in control and fertilised plots, and annual precipitation for each site was generated using interpolated monthly climate data (SILO; Jeffrey et al. 2001, available online). These data are interpolated for each site from surrounding meteorological stations and are hence, necessarily, an estimate of site rainfall. Because sites vary in their growing season timing and duration, we estimated 'growing season period' of all sites using the expert opinion of Nutrient Network plot leaders. This was the month when rainfall for the current season's growth generally begins to the month of peak biomass (when material was harvested by site investigators). Proportion of yearly GSP to long-term mean GSP can better explain inter-annual variation in primary production than total annual precipitation (Bai et al. 2004; Swemmer et al. 2007; Hovenden et al. 2014). We then calculated mean GSP using data for the period 1950-2013. For each year of study, deviation from the mean GSP at each site was calculated as: $GSP_{(t)}$ = (year(t) GSP / mean GSP). We confine our analyses to the pre-fertilization year and the five years of annual nutrient addition. We then log transformed these data and divided them by two standard deviations so they could be included within the model. Dividing by two standard deviations standardizes the covariate so that the magnitude of GSP effect (a continuous covariate) can be compared with binary coefficients (i.e. nutrient addition treatment) (Gelman & Hill 2007).

Analysis

In total we ran five hierarchical Bayesian models to examine NPK and GSP effects on rates of change in biomass production, rates of change in native and exotic cover, and differences in native and exotic richness. When modelling rates of change in biomass and cover changes, we use a modified version of a Bayesian hierarchical model advocated by Camac et al. (2015). This model allowed us to explicitly model how experimental nutrient addition and the temporal variability in GSP affected rates of change. We used this modelling approach because commonly used methods such as repeated measures ANOVA and GLMs (with random effects for time) do not provide estimates of rates, rather they model differences or ratios of state variables for control and manipulated groups observed at some time(s), with non-independence of observations through time accounted for by computation of appropriate F-ratios (Gelman & Hill 2007). Modelling covariate effects on rates, rather than differences amongst groups, has the advantages of examining how the underlying process of change is affected by covariates, and as such provides information on both the direction and speed at which changes are occurring (Camac et al. 2015). Detailed descriptions of the models used in these study can be found in Appendix S1.

Results

Over six years, live above-ground biomass in grasslands varied substantially across plots, sites and years (Fig. 1). The alpine grassland (Bogong) consistently had the highest primary production, while the semi-arid grassland at Mt Caroline exhibited the lowest (Table 1, Fig. 1). Annual growing season precipitation across the study period varied at most sites from 50-150% of mean GSP (Fig. 1), with Mt Caroline consistently at (or below) mean GSP. Native (Fig. 2) and exotic cover (Fig. 3) also showed much variation across plots, sites, and years, with the alpine grassland (Bogong) consistently having higher native cover than all other grasslands, and the lowest exotic cover.

Grassland biomass production

Rates of biomass production was most variable between sites (σ_{site} = 0.43, 95% BCI: 0.13 to 1.33), followed by between years (σ_{census} = 0.12, 95% BCI: 0.01 to 0.43) and then between plots (σ_{plot} = 0.043, 95% BCI: 0.002 to 0.43). Log rates of biomass production in control plots at the long-term mean GSP conditions (i.e. the intercepts) were strongly positive at Bogong but were not significantly different from zero for the other three sites (Fig. 4). This indicates that when sites are exposed to long-term GSP conditions, Bogong experiences a faster rate of biomass accumulation relative to the other sites. Annual rates of biomass production were positively correlated with GSP (Fig. 4). For example, at a GSP of 0.4, Kinypanial is predicted to have a rate of biomass production of 0.64 – a rate that would see biomass decline by 36% relative to average GSP years. By contrast, at a GSP of 1.7, the expected rate is predicted to be at least three times higher at 2.2. We detected no significant effect of NPK on biomass production, nor did we detect a significant interaction between NPK and GSP (Fig. 1, Fig. 4).

Native and exotic cover

Like the biomass data, rates of native and exotic cover change were more variable between sites (σ_{site}; Natives: 0.65, 95% BCI: 0.17 to 2.0; Exotics: 0.94, 95% BCI: 0.31 to 2.60) than between plots (σ_{plot}; Natives: 0.38, 95% CI: 0.07 to 0.55; Exotics: 0.12, 95% BCI: 0.01 to 0.32) or between censuses (σ_{census}; Natives: 0.20, 95% BCI: 0.005 to 0.69; Exotics: 0.17, 95% BCI: 0.01 to 0.67). At long-term GSP, mean log rates of native cover change in control plots were positive at Bogong (Fig. 5c) and not significantly different from zero at Kinypanial and Mt Caroline (Fig. 5g, i). For exotic species, cover rate change was strongly negative at Bogong (Fig. 5d) and strongly positive at Burrawan (Fig 5f), but not significant at Kinypanial and Mt Caroline (i.e. credible intervals overlapped zero) (Fig. 5h, j).

Nutrient addition affected rates of cover change in natives and exotics differently (Fig. 5). In natives, rates of cover change declined with NPK addition, while in exotics no significant effect was detected. The consequence of this was that native cover increased at a slower rate in NPK plots relative to control plots (Fig. 5). GSP marginally increased the rate of native cover expansion. For both native and exotic cover, we detected no significant interaction between NPK and GSP (Fig. 5).

Native and exotic species richness

The number of native and exotic species was most variable between sites (σ_{site}; Natives: 0.97, 95% BCI: 0.36 to 2.8; Exotics: 0.81, 95% BCI: 0.3 to 2.3) then either plot (σ_{plot}; Natives: 0.12, 95% CI: 0.01 to 0.25; Exotics: 0.11, 95% BCI: 0.01 to 0.29) or census (σ_{census}; Natives: 0.26, 95% BCI: 0.11 to 0.62; Exotics: 0.28, 95% BCI: 0.08 to 0.72). Bogong, on average, had three times as many native species per plot (15.4) relative to the other three sites, which all had approximately 5 species (Fig 6). By contrast, Bogong and Burrawan had on average the fewest exotic species per plot (1.7 and 1.8, respectively) while Kinypanial had 3.8 and Mt Caroline had 4.5.

Nutrient addition had a negative effect on the number of native species per plot (Fig. 6a), whereas it had a marginally positive effect on number of exotic species. We detected no significant effect of GSP or its interaction with NPK on either native or exotic richness (Fig. 6a).

Discussion

Rates of annual live biomass production in the four Australian grasslands we studied were strongly affected by GSP but not nutrient (NPK) addition. We did not detect a significant interaction between GSP and nutrient addition. Despite our prediction that Australian grasslands might be very responsive to the addition of limiting nutrients, given they occur on highly weathered, nutrient-poor soils (Specht & Specht 1999; Orians & Milewski 2007), we found that live biomass production was not significantly affected by nutrient addition. This is in stark contrast to grasslands elsewhere (Elser et al. 2007), including many of the sites in the Nutrient Network experiment of which our grasslands are a part (Fay et al. 2015) which have shown strong positive responses to nutrient addition. Instead, annual rates of biomass were governed more by interannual rainfall variability, with rates of biomass production strongly increasing with increasing GSP.

Differences in temporal and spatial responsiveness in biomass production of grasslands to nutrients and rainfall have been well-documented (e.g. Harpole et al. 2007; Lu et al. 2014). Typically, the maximum sensitivity of biomass production to interannual precipitation variability has been found at sites with intermediate levels of precipitation (Knapp & Smith 2001; Hsu et al. 2012) while at xeric sites, low temporal sensitivity of biomass production has been attributed to traits of the dominant species that often exhibit low responsiveness to resource pulses (Lauenroth & Sala 1992; Hall et al. 2011). Indeed, infertile ecosystems are typically dominated by stress-adapted plants where strategies of nutrient retention and tissue protection are fundamentally associated with slow growth, long individual lifespans, and persistent shoot and root systems capable of withstanding significant seasonal and interannual climate variation (Grime et al. 2008; Morton et al. 2011; Hayes et al. 2014). We did not observe strong nutrient limitation to growth response rate in the Australian grasslands we studied. Rather, the rate of annual biomass production was sensitive to the variation observed in interannual variation in GSP. Grassland productivity falls with declining GSP and is not significantly offset by nutrient addition. That said, in our low rainfall site where annuals are an important contributor to biomass (Mt Caroline), nutrient addition can elicit biomass increases (Fig. 1), with exotic species most likely contributing to this response (Fig. 2, 3). Nutrient enrichment is widely associated with dominance by exotic annuals (Huenneke et al. 1990) and it hints that there are important, site-specific responses that obscure general patterns. Our data do suggest, however, that altered precipitation regimes will exert strong impacts on the growth of Australian grasslands, irrespective of soil fertility. This accords with the proposition from Morton et al. (2011) that in Australia, soil moisture (ultimately driven by GSP) governs the tempo and mode of opportunities for plants to persist and thereby shapes the suite of life histories present and the productivity of the system.

While the interaction between water and nutrient availability on biomass production is important outside of Australia (Lee et al. 2010; Gong et al. 2011; Hall et al. 2011; Yahdjian et al. 2011), we found no such interaction between annual nutrient addition and GSP on rates of biomass production. Nutrients were added annually for five years at the rate of 10 g m^{-2} (for each of N, P and K), but it is not known how such additions raised the nutrient status of soils. Elsewhere, we have shown that nutrient co-limitation by N, P and K is common for biomass production across the world's grasslands (Fay et al. 2015), so it is likely that our treatments have increased resources (to potentially super-abundant levels). However, our data show weak evidence of additive fertilizer effects on rates of annual live biomass production across our sites, and little evidence for threshold responses; rather, there is a strong link to growing season precipitation. A possible explanation for the lack of a nutrient *x* water interaction may relate to the complex effects that these factors can have on water use efficiency (WUE) and nitrogen use efficiency (NUE). WUE tends to decrease with increasing precipitation but increases with increasing nitrogen availability (Burke et al. 1997; Hooper & Johnson 1999; Bai et al. 2008). Furthermore, nitrogen addition does not always lead to increased primary production in grasslands because there is a tradeoff between enhanced plant nitrogen uptake and decreased NUE (Lu et al. 2014). In this case, plant nitrogen uptake under fertilized conditions can lead to changes in plant nitrogen concentrations (i.e. higher leaf N; Bracken et al. 2015) rather than observed changes in community biomass (Lu et al. 2014). Hence, variation in GSP, combined with nutrient addition, likely affect WUE and NUE in Australian grasslands in ways that are not simply predicted by the additive effects of individual drivers.

Species-specific nutrient use strategies of plants, and their response to resource amendment, appear to play an important role in Australian grasslands (Specht 1963; McIntyre & Lavorel 1994) as they do elsewhere (Gong et al. 2011; Hall et al. 2011; Prober & Wiehl 2012; Hallet et al. 2014; Lu et al. 2014; Lai et al. 2015; Seabloom et al. 2015). Our modelled rate of cover change showed that native cover responded positively to GSP and negatively to nutrient addition, and species richness declined with nutrient addition, i.e. native species were lost over time. Rates of exotic cover and richness change to nutrient addition were detected, although both covariates explained little overall variation. The direction of the covariates accords with studies that show that Australian native grassland species can be negatively affected by nutrient addition (Dorrough & Scroggie 2008) and exotics are more positively affected (Price & Morgan 2007). The contrasting behaviors of native and exotic species can be attributed to differences in their evolutionary history and their resulting pre-adaptations to landscapes with different agricultural settlement histories and soil fertility (McIntyre & Lavorel 1994; Hopper 2009; Prober & Wiehl 2012; Seabloom et al. 2015). Our data suggest that to model the effects of land-atmosphere interactions, particularly ecosystem productivity and plant diversity, models need to include seasonal rainfall variability and species origin if they are to accurately predict responses (McIntyre & Lavorel 1993; Prober & Wiehl 2012; Hovenden et al. 2014).

Conclusions

In order to predict trajectories of vegetation under global change, we need to understand how resources influence rates and direction of vegetation change (Camac et al. 2015). Several studies show that nutrient addition can increase grassland productivity, particularly in wetter years (e.g. in South African grasslands; Swemmer et al. 2007) or irrigated plots (Li et al. 2011), but this generalization did not hold for our Australian grassland study sites. We found that rates of annual live biomass production were positively affected by both GSP but we did not detect an effect of nutrient (NPK) addition across our four study sites. Furthermore, we did not detect a significant interaction between GSP and nutrient addition. Climate variability, primarily seasonal variability in precipitation, therefore appears to be the principal driver of rates of biomass production in the Australian grasslands we studied, as also observed by Hovenden et al. (2014), with soil nutrients acting as an important secondary driver that negatively affects native species cover and richness. The importance of these drivers, and their interaction, for this region's productivity has until now only been inferred because appropriate data for Australian grasslands have been lacking (White et al. 2014). The positive relationship between interannual variation in biomass production and temporal variability in GSP predicts that altered precipitation regimes will exert strong impacts on the growth of grasslands, and that the response will vary between native and exotic species. These findings should be incorporated into the prediction and modelling of how grassland ecosystems respond to climate changes and to short-term fluctuations of rainfall.

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References

Bai, Y.F., Han, X.G., Wu, J.G., Chen, Z.Z. & Li, L.H. 2004. Ecosystem stability and compensatory effects in the Inner Mongolia grassland. *Nature* 431: 181-184.

Borer, E.T., Seabloom, E.W., Gruner, D.S., Harpole, W.S., Hillebrand, H., Lind, E.M., Adler, P.B., Alberti, J., Anderson, T.M., Bakker, J.B., Biederman, L., Blumenthal, D., Brown, C.S., Brudvig, L.A., Buckley, Y.M., Cadotte, M., Chu, C., Cleland, E.E., Crawley, M.J., Daleo, P., Damschen, E.I., Davies, K.F., DeCrappeo, N.M., Du, G., Firn, J., Hautier, Y., Heckman, R.W., Hector, A., HilleRisLambers, J., Iribarne, O., Klein, J.A., Knops, J.M.H., La Pierre, K.J., Leakey, A.D.B., Li, W., MacDougall, A.S., McCulley, R.L., Melbourne, B.A., Mitchell, C.E., Moore, J.L., Mortensen, B., O'Halloran, L.R., Orrock, J.L., Pascual, J., Prober, S.M., Pyke, D.A., Risch, A.C., Schuetz, M., Smith, M.D., Stevens, C.J., Sullivan, L.L., Williams ,R.J., Wragg, P.D., Wright, J.P. & Yang, L.H. 2014a. Herbivores and nutrients control grassland plant diversity via light limitation. *Nature* 508: 517-520.

Borer, E.T., Harpole, W.S., Adler, P.B., Lind, E.M., Orrock, J.L., Seabloom, E.W. & Smith, M.D. 2014b. Finding generality in ecology: a model for globally distributed experiments. *Methods in Ecology and Evolution* 5: 65-73.

Bracken, M.E.S., Hillebrand, H., Borer, E.T., Seabloom, E.W., Cebrian, J., Cleland, E.E., Elser, J.J., Gruner, D.S., Harpole, W.S., Ngai, J.T. & Smith, J.E. 2015. Signatures of nutrient limitation and co-limitation: responses of autotroph internal nutrient concentrations to nitrogen and phosphorus additions. *Oikos* 124: 113-121.

Burke, I., Lauenroth, W.K. & Parton, W.J. 1997. Regional and temporal variation in net primary production and nitrogen mineralisation in grasslands. *Ecology* 78: 1330–1340.

Camac, J.S., Williams, R.J., Wahren, C-H., Jarrad, F.C., Hoffmann, A.A. & Vesk, P.A. 2015. Modeling rates of life form cover change in burned and unburned alpine heathland subject to experimental warming. *Oecologia* 178:615-628.

Dorrough, J. & Scroggie, M.P. 2008. Plant responses to agricultural intensification. *Journal of Applied Ecology* 45: 1274–1283.

Dukes, J.S., Chiariello, N.R., Cleland, E.E., Moore, L.A., Shaw, M.R., Thayer, S., Tobeck, T., Mooney, H.A. & Field, C.B. 2005. Responses of grassland production to single and multiple global environmental changes. *PLoS Biology* 3: e319.

Dwyer, J.M., Hobbs, R.J., Wainwright, C.E. & Mayfield, M.M. 2015. Climate moderates release from nutrient limitation in natural annual plant communities. *Global Ecology and Biogeography* 24: 549-561.

Elser, J.J., Bracken, M.E., Cleland, E.E., Gruner, D.S., Harpole, W.S., Hillebrand, H., Ngai, J.T., Seabloom, E.W., Shurin, J.B. & Smith, J.E. 2007. Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecology Letters* 10: 1135-1142.

Fay, P.A., Prober, S.M., Harpole, W.S., Knops, J.M.H., Bakker, J.D., Borer, E.T., MacDougall, A.S., Seabloom, E., Wragg, P.D., Blumenthal, D.M., Buckley, Y.B., Chu, C., Cleland, E.E., Collins, S.L., Davies, K.F., Du, G., Feng, X., Firn, J., Gruner, D.S., Hagenah, N., Hautier, Y., Heckman, R.W., Jin, V.L., Kirkman, K.P., Klein, J., Ladwig, L.M., Li, Q., McCulley, R.L., Melbourne, B.A., Mitchell, C.E., Moore, J.L., Morgan, J.W., Risch, C., Schütz, M., Stevens, C.J., Wedin, D.A. & Yang, L.H. 2015. Grassland productivity limited by multiple nutrients. *Nature Plants* 15080.

Gelman, A. & Hill, J. 2007. *Data analysis using regression and multilevel/hierarchical models*. Cambridge University Press, Cambridge.

Going, B.M., HilleRisLambers, J. & Levine, J.M. 2009. Abiotic and biotic resistance to grass invasion in serpentine annual plant communities. *Oecologia* 159: 839-847.

Gong, X.Y., Chen, Q., Lin, S., Brueck, H., Dittert, K., Taube, F. & Schnyder, H. 2011. Tradeoffs between nitrogen- and water-use efficiency in dominant species of the semiarid steppe of Inner Mongolia. *Plant and Soil* 340: 227-238.

Grime, J.P., Fridley, J.D., Askew, A.P., Thompson, K., Hodgson, J.G. & Bennett, C.R. 2008. Long-term resistance to simulated climate change in an infertile grassland. *Proceedings of the National Academy of Sciences* 105: 10028– 10032.

Hall, S.J., Sponseller, R.A., Grimm, N.B., Huber, D., Kaye, J.P., Clark, C. & Collins, S.L. 2011. Ecosystem response to nutrient enrichment across an urban airshed in the Sonoran Desert. *Ecological Applications* 21: 640-660.

Hallett, L.M., Hsu, J.S., Cleland, E.E., Collins, S.L., Dickson, T.L., Farrer, E.C., Gherardi, L.A., Gross, K.L., Hobbs, R.J., Turnbull, L. & Suding, K.N. 2014 Biotic mechanisms of community stability shift along a precipitation gradient. *Ecology* 95: 1693–1700.

Harpole, W.S., Potts, D.L. & Suding, K.N. 2007. Ecosystem responses to water and nitrogen amendment in a Californian grassland. *Global Change Biology* 13: 2341-2348.

Harpole, W.S., Ngai, J.T., Cleland, E.E., Seabloom, E.W., Borer, E.T., Bracken, M.E.S., Elser, J.J., Gruner, D.S, Hillebrand, H., Shurin, J.B. & Smith, J.E. 2011 Nutrient co-limitation of primary producer communities. *Ecology Letters* 14: 852-862.

Harpole, W.S. & Tilman, D. 2007. Grassland species loss resulting from reduced niche dimension. *Nature* 446: 791-793.

Hayes, P., Turner, B.L., Lambers, H. & Laliberte, E. 2014. Foliar nutrient concentrations and resorption efficiency in plants of contrasting nutrient-acquisition strategies along a 2-million-year dune chronosequence. *Journal of Ecology* 102: 396–410.

Huenneke, L.F., Hamburg, S.P., Koide, R., Mooney, H.A. & Vitousek, P.M. 1991. Effects of soil resources on plant invasion and community structure in Californian serpentine grassland. *Ecology* 71: 478-491.

Hopper, S.D. 2009. OCBIL theory: towards an integrated understanding of the evolution, ecology and conservation of biodiversity on old, climatically buffered, infertile landscapes. *Plant and Soil* 322: 49-86.

Hooper, D.U. & Johnson, L. 1999. Nitrogen limitation in dryland ecosystems: responses to geographical and temporal variation in precipitation. *Biogeochemistry* 46: 247–293.

Hovenden, M.J., Newton, P.C.D. & Wills, K.E. 2014. Seasonal not annual rainfall determines grassland biomass response to carbon dioxide. *Nature* 511: 583-586.

Hsu, J.S., Powell, J. & Adler, P.B. 2012. Sensitivity of mean annual primary production to precipitation. *Global Change Biology* 18: 2246-2255.

Jeffrey, S.J., Carter, J.O., Moodie, K.P. & Beswick, A.R. 2001. Using spatial interpolation to construct a comprehensive archive of Australian climate data. *Environmental Modelling and Software* 16: 309–330. Available at http://www.longpaddock.qld.gov.au/silo/

Knapp, A.K., Briggs, J.M., Hartnett, D.C. & Collins, S.L. 1998. *Grassland dynamics: long-term ecological research in tallgrass prairie.* Oxford University Press, New York.

Knapp, A.K., Briggs, J.M. & Koelliker, J.K. 2001. Frequency and extent of water limitation to primary production in a mesic temperate grassland. *Ecosystems* 4: 19-28.

Knapp, A.K. & Smith, M.D. 2001. Variation among biomes in temporal dynamics of aboveground primary production. *Science* 291: 481-484.

Lai, H.R., Mayfield, M.M., Gay-des-combes, J.M., Spiegelberger, T. & Dwyer, J.M. 2015 Distinct invasion strategies operating within a natural annual plant system. *Ecology Letters* 18: 336-346.

Laliberte, E., Zemunik, G. & Turner, B.J. 2014. Environmental filtering explains variation in plant diversity along resource gradients. *Science* 345: 1602-1605.

Lambers, H., Brundrett, M.C., Raven, J.A. & Hopper, S.D. 2010. Plant mineral nutrition in ancient landscapes: high plant species diversity on infertile soils is linked to functional diversity for nutritional strategies. *Plant and Soil* 334: 11-31.

Lauenroth, W.K. & Sala, O.E. 1992. Long term forage production of North American shortgrass steppe. *Ecological Applications* 2: 397-403.

Lee, M., Manning, P., Rist, J., Power, S.A. & Marsh, C. 2010. A global comparison of grassland biomass responses to CO_2 and nitrogen enrichment. *Philosophical Transactions of the Royal Society* B 365: 2047–2056.

Leeper, G.W. & Uren, N.C. 1993. *Soil science: an introduction*. Melbourne University Press, Carlton.

Li, J., Lin, S., Taube, F., Pan, Q. & Dittert, K. 2011. Above and belowground net primary productivity of grassland influenced by supplemental water and nitrogen in Inner Mongolia. *Plant and Soil* 340: 253–264.

Lu, X-T., Dijkstra, F.A., Kong, D-L., Wang, Z-W. & Han, X-G. 2014. Plant nitrogen uptake drives responses of productivity to nitrogen and water addition in a grassland. *Scientific Reports* 4: 4817 doi:10.1038/srep04817.

McIntyre, S. & Lavorel, S. 1994. Predicting richness of native, rare, and exotic plants in response to habitat and disturbance variables across a variegated landscape. *Conservation Biology* 8: 521–531.

McMahon, T.A., Finlayson, B., Haines, A.T. & Srikanthan, R. 1992. Global runoff – continental comparisons of annual flows and peak discharges. Cantena Paperback, Cremlingen-Destedt.

Morton, S.R., Stafford Smith, D.M., Dickman, C.R., Dunkerley, D.L., Friedel, M.H., McAllister, R.R.J., Reid, J.R.W., Roshier, D.A., Smith, M.A., Walsh, F.J., Wardle, G.M., Watson, I.W.& Westoby, M. 2011. A fresh framework for the ecology of arid Australia. *Journal of Arid Environments* 75: 313-329.

Orians, G.H. & Milewski, A.V. 2007. Ecology of Australia: the effects of nutrient-poor soils and intense fires. *Biological Reviews* 82: 393–423.

Paruelo, J.M., Lauenroth, W.K., Burke, I.C. & Sala, O.E. 1999 Grassland precipitation-use efficiency varies across a resource gradient. *Ecosystems* 2: 64–68.

Poorter, H. & Nagel, O. 2000. The role of biomass allocation in the growth responses of plants to different levels of light, CO2, nutrients and water: a quantitative review. *Australian Journal of Plant Physiology* 27: 595-607.

Price, J.N. & Morgan, J.W. 2007. Vegetation dynamics following resource manipulations in herb-rich woodland. *Plant Ecology* 188: 29-37.

Prober, S.M. & Wiehl, G. 2012. Relationships among soil fertility, native plant diversity and exotic plant abundance inform restoration if forb-rich eucalypt woodlands. *Diversity and Distributions* 18: 795-807.

Reich, P.B. & Hobbie, S.E. 2013. Decade-long soil nitrogen constraint on the CO$_2$ fertilization of plant biomass. *Nature Climate Change* 3: 278-282.

Sala, O.E., Parton, W.J., Joyce, L.A. & Lauenroth, W.K. 1988. Primary production of the Central Grassland region of the United States. *Ecology* 69: 40-45.

Sala, O.E., Gherardi, L.A., Reichmann, L., Jobbágy, E. & Peters, D. 2012. Legacies of precipitation fluctuations on primary production: theory and data synthesis. *Philosophical Transactions of the Royal Society B* 367: 3135-3144.

Seabloom, E.W., Borer, E.T., Buckley, Y.B., Cleland, E.E., Davies, K.F., Firn, J., Harpole, W.S., Hautier, Y,., Lind, E.M., MacDougall, A.S., Orrock, J.L., Prober, S.M., Adler, P.B., Anderson, T.M., Bakker, J.D., Biederman, L.A., Blumenthal, D.M., Brown, C.S., Brudvig, L.A., Cadotte, M., Chu, C., Cottingham, K.L., Crawley, M.J., Damschen, E.I., D'Antonio, C.M., DeCrappeo, N.M., Du, G., Fay, P.A., Frater, P., Gruner, D.S., Hagenah, N., Hector, A., Hillebrand, H., Hofmockel, K.S., Humphries, H.C., Jin, V.L., Kay, A., Kirkman, K.P., Klein, J.A., Knops, J.M.H., La Pierre, K.J., Ladwig, L., Lambrinos, J.G., Li, Q., Li, W., Marushia, R., McCulley, R.L., Melbourne, B.A., Mitchell, C.E., Moore, J.L., Morgan, J., Mortensen, B.L., O'Halloran, L.R., Pyke, D.A., Risch, A.C., Sankaran, M., Schuetz, M, Simonsen, A., Smith, M.D., Stevens, C.J., Sullivan, L., Wolkovich, E., Wragg, P.D., Wright, J. & Yang, L. 2015. Plant species' origin predicts dominance and response to nutrient enrichment and herbivores in global grasslands. *Nature Communications* **6**: 7710, doi:10.1038/ncomms8710

Seastedt, T.R., Hayden, B.P., Owensby, C.E. & Knapp, A.K. 1998. Climate change, elevated CO$_2$, and predictive modelling: past and future climate change scenarios for the tallgrass prairie. In: Knapp AK, Briggs JM, Hartnett DC, Collins SL (eds) *Grassland dynamics: long-term ecological research in tallgrass prairie*. Oxford University Press, New York, pp. 283-300.

Smallbone, L.T., Lunt, I.D. & Prober, S.M. 2008. Soil nitrate promotes growth of an exotic grass more than native forbs. *Ecological Management and Restoration* 9: 60-63.

Specht, R.L. 1963. Dark Island heath (Ninety-mile Plain, South Australia). VII. The effect of fertilizers on composition and growth, 1950-1960. *Australian Journal of Botany* 11: 67-94.

Specht, R.L. & Specht, A. 1999. *Australian plant communities: dynamics of structure, growth and biodiversity*. Oxford University Press, South Melbourne.

Swemmer, A.M., Knapp, A.K. & Snyman, H.A. 2007. Intra-seasonal precipitation patterns and above-ground productivity in three perennial grasslands. *Journal of Ecology* 95: 780–788.

van Etten, E.J.B. 2009. Inter-annual rainfall variability of arid Australia: greater than elsewhere? *Australian Geographer* 40: 109-120.

Vines, R.G., Noble, J.C. & Marsden, S.G. 2004. Australian rainfall patterns and the southern oscillation. 1. A continental perspective. *Pacific Conservation Biology* 10: 28-48.

Wang, C.H., Wan, S.Q., Xing, X.R., Zhang, L. & Han, X.G. 2006. Temperature and soil moisture interactively affected soil N net mineralization in temperate grasslands in Northern China. *Soil Biology and Biochemistry* 38: 1101-1110.

White, A., Orr, D., Novelly, P. & Bastin, G. 2014. Tussock grasslands. In: Lindenmayer D, Burns E, Thurgate N, Lowe, A (eds) *Biodiversity and environmental change: monitoring, challenges and direction*. CSIRO Publishing, Collingwood, pp 479-517.

Yahdjian, L., Gherardi, L. & Sala, O.E. 2011. Nitrogen limitation in arid-subhumid ecosystems: a meta-analysis of fertilization studies. *Journal of Arid Environments* 75: 675-680.

Yang, Y., Fang, J., Ma, W. & Wang, W. 2008. Relationship between variability in aboveground net primary production and precipitation in global grasslands. *Geophysical Research Letters* 35: L23710, doi:10.1029/2008GL035408

Appendix S1: Model descriptions

Table 1. Description of vegetation, climate and soils of the study sites. Rainfall data are from nearest meteorological station and accessed from the Australian Weather Bureau (www.bom.gov.au). Soil nutrient data are from samples collected prior to the application of NPK (presented in Fay et al. 2015).

MAP = mean annual precipitation, GSP = mean growing season precipitation, MAT = mean annual temperature, GSPCV = coefficient of variation of mean growing season precipitation, ANPP = mean above-ground net primary productivity of control plots over the duration of the experiment.

Site Name	Location (decimal degrees)	Grassland Type	MAP (mm)	GSP (mm)	MAT (°C)	GSPCV (%)	Soil Texture	Soil N (%)	Soil P (ppm)	Soil K (ppm)	ANPP (g m^{-2})
Bogong	36.85 S, 147.25 E	C_3, dominated by perennial grasses and forbs	1217	864	7.2	36	Sandy loam	0.06	44.3	189	474
Burrawan	27.75 S, 151.15 E	C_4, dominated by perennial grasses	600	450	18.4	30	Sandy loam	0.08	17.4	76	247
Kinypanial	36.20 S, 143.75 E	C_3, dominated by annual and perennial grasses	395	226	15.5	32	Clay loam	0.12	10.2	456	204
Mt Caroline	31.80 S, 117.60 E	C_3, dominated by annual grasses and forbs	352	237	17.6	27	Loamy sand	0.09	9.3	191	105

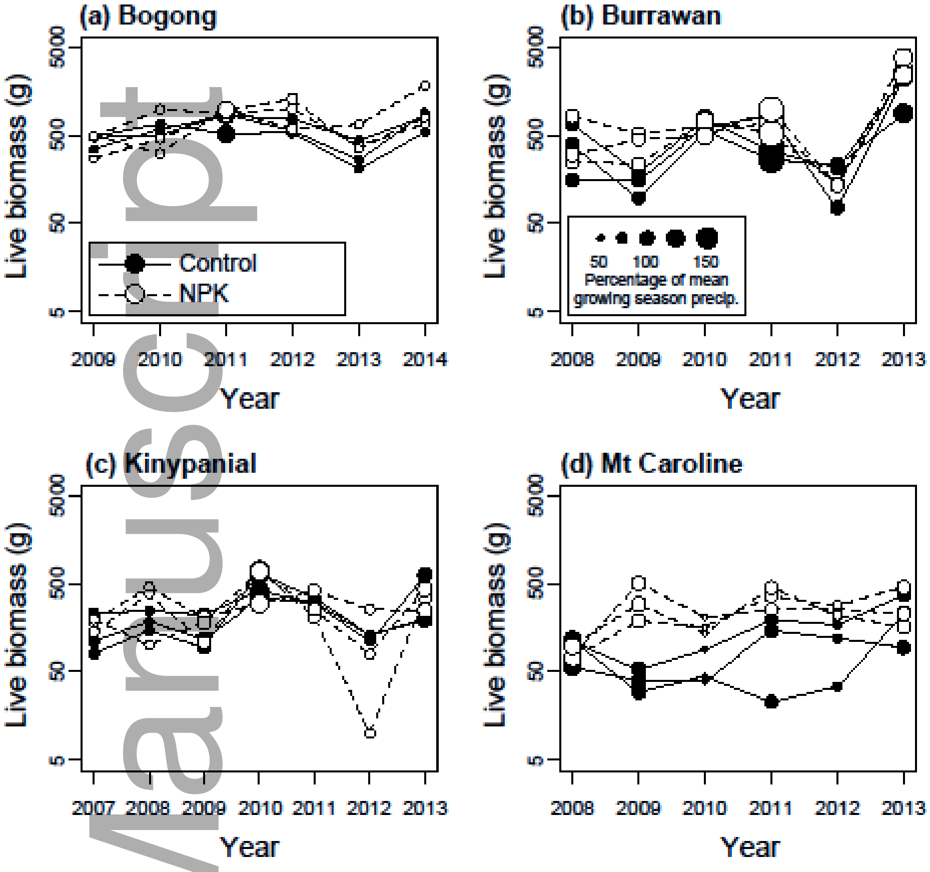

Fig. 1. Observed live biomass (g /m^2) in each of three replicate plots at four Australian grasslands. Solid line with solid circle: unfertilised plots; dashed line with open circle: fertilised with NPK from year 2 onwards. The size of the data point represents deviation from mean growing season precipitation, as indicated.

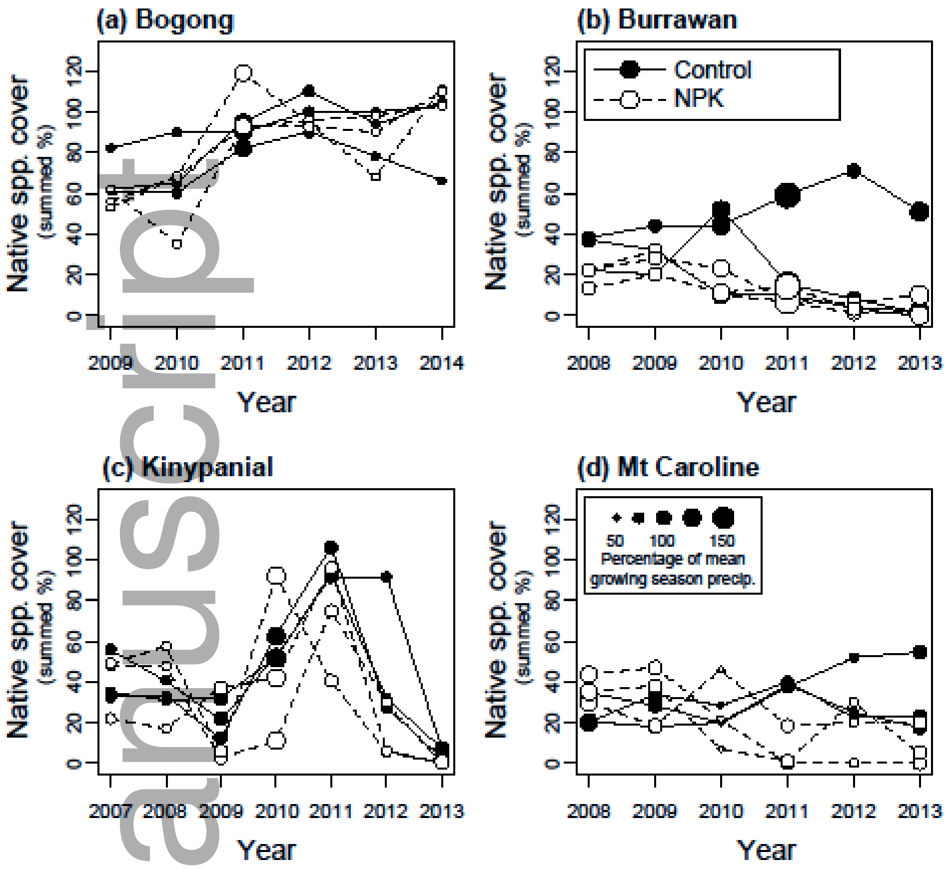

Fig. 2. Observed total native cover (summed percent /m^2) in each of three replicate plots at four Australian grasslands. Solid line with solid circle: unfertilised plots; dashed line with open circle: fertilised with NPK from year 2 onwards. The size of the data point represents deviation from mean growing season precipitation, as indicated.

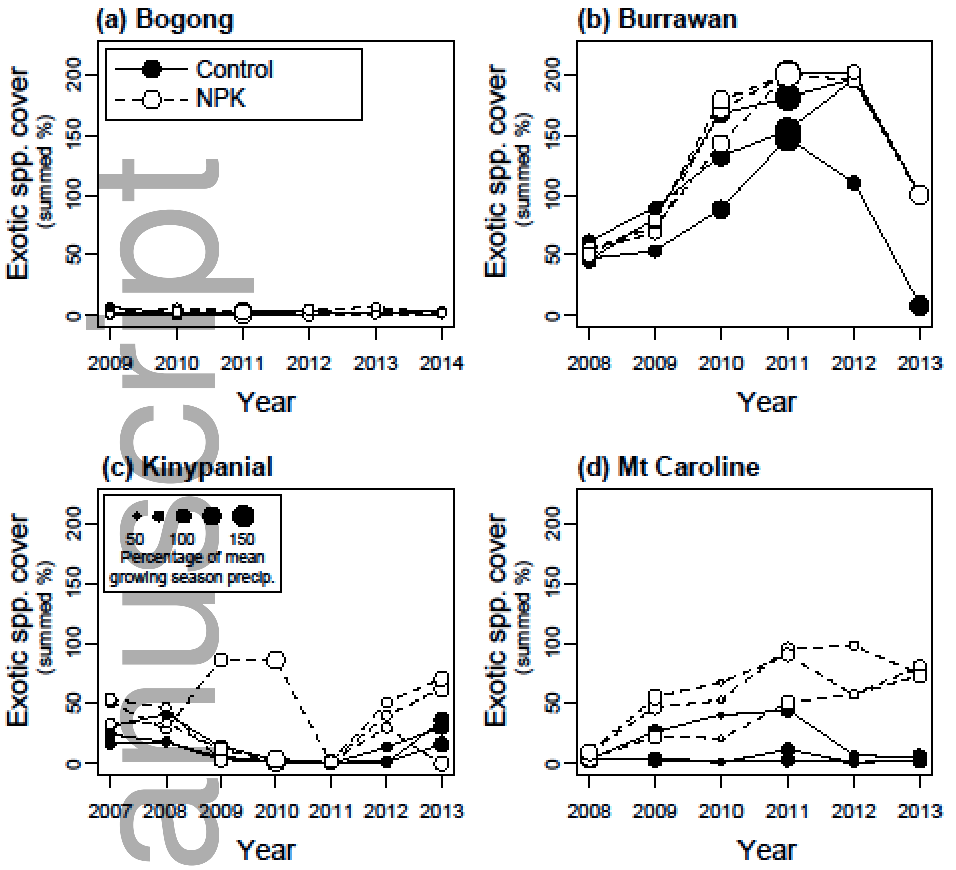

Fig. 3. Observed total exotic cover (summed percent/m^2) in each of three replicate plots at four Australian grasslands. Solid line with solid circle: unfertilised plots; dashed line with open circle: fertilised with NPK from year 2 onwards. The size of the data point represents deviation from mean growing season precipitation, as indicated.

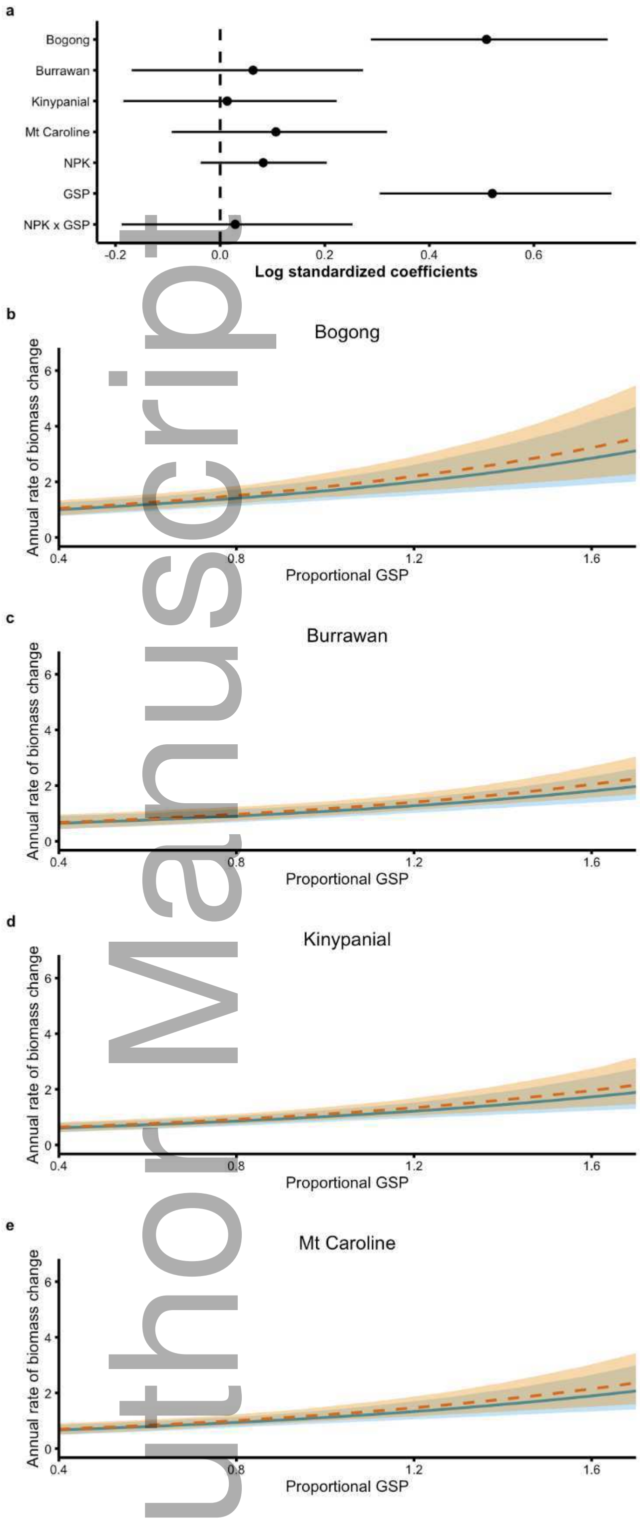

Fig. 4. (a) Regression coefficients ± 95 (thin line) Bayesian Credible Intervals for site random effects and each fixed effect in the model predicting annual rate of live biomass production. The Y-axis (b-e) shows the site intercepts (Bogong, Burrawan, Kinypanial and Mt Caroline) interpreted as the log mean annual rate of biomass production in control conditions at mean long-term growing season precipitation (GSP). NPK, GSP and NPK x GSP are the modelled effects of NPK addition, GSP and their associated interaction on rates of live biomass production, respectively. Response curves (back-transformed to a proportional change) illustrating how rates of live above-ground biomass vary with both NPK treatment and GSP. Dashed orange lines = NPK conditions, solid blue lines = Control; 95% credible intervals shown

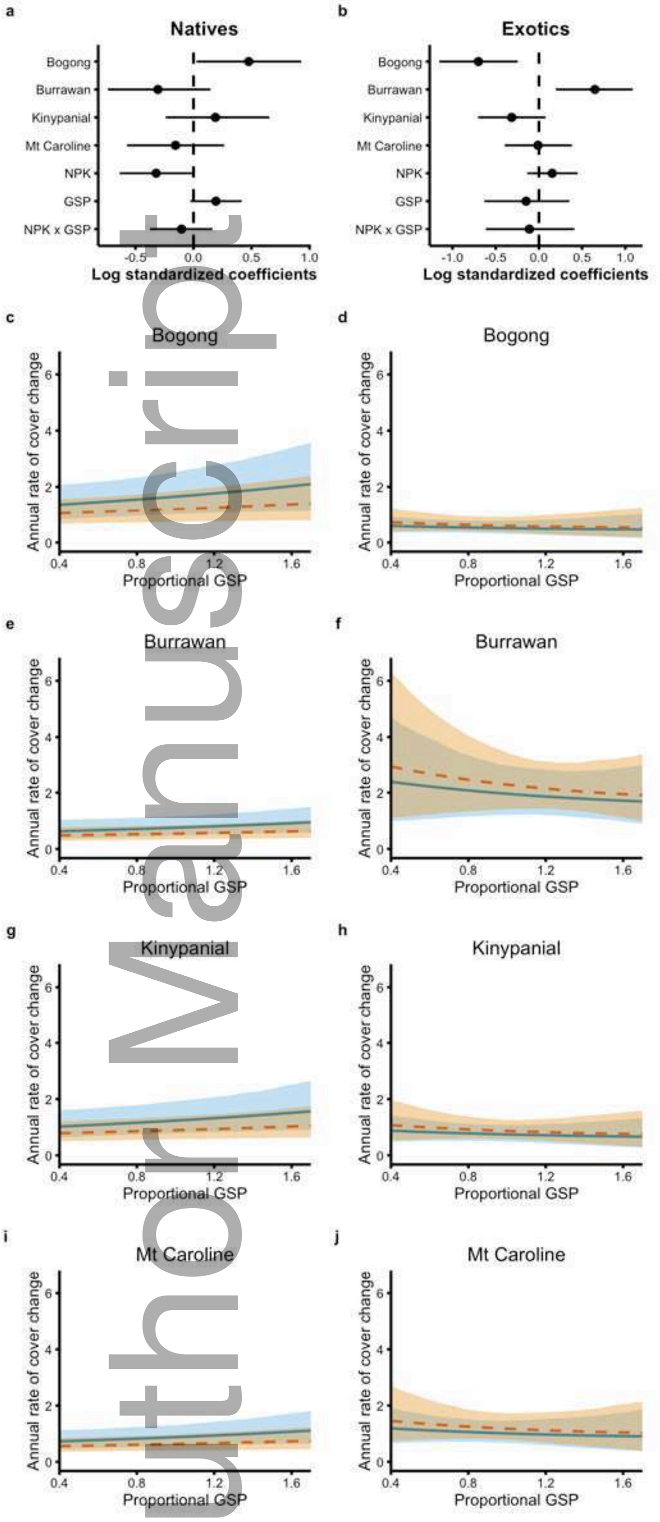

Fig. 5 Regression coefficients ± 95 Bayesian Credible Intervals for site random effects and each fixed effect in the model predicting annual rate of native (a) and exotic (b) cover change. The Y-axis shows the site intercepts (Bogong, Burrawan, Kinypanial and Mt Caroline) interpreted as the log mean annual rate of cover change in control conditions at mean long-term growing season precipitation (GSP). NPK, GSP and NPK x GSP are the modelled effects of NPK addition, GSP and their associated interaction on rates of cover, respectively. Response curves (back-transformed to a proportional change) illustrating how rates of cover change of both natives (c,e,g,i) and exotics (d,f,h,j) vary with both NPK treatment and GSP. Dashed orange lines = NPK conditions, solid blue lines = Control; 95% credible intervals shown

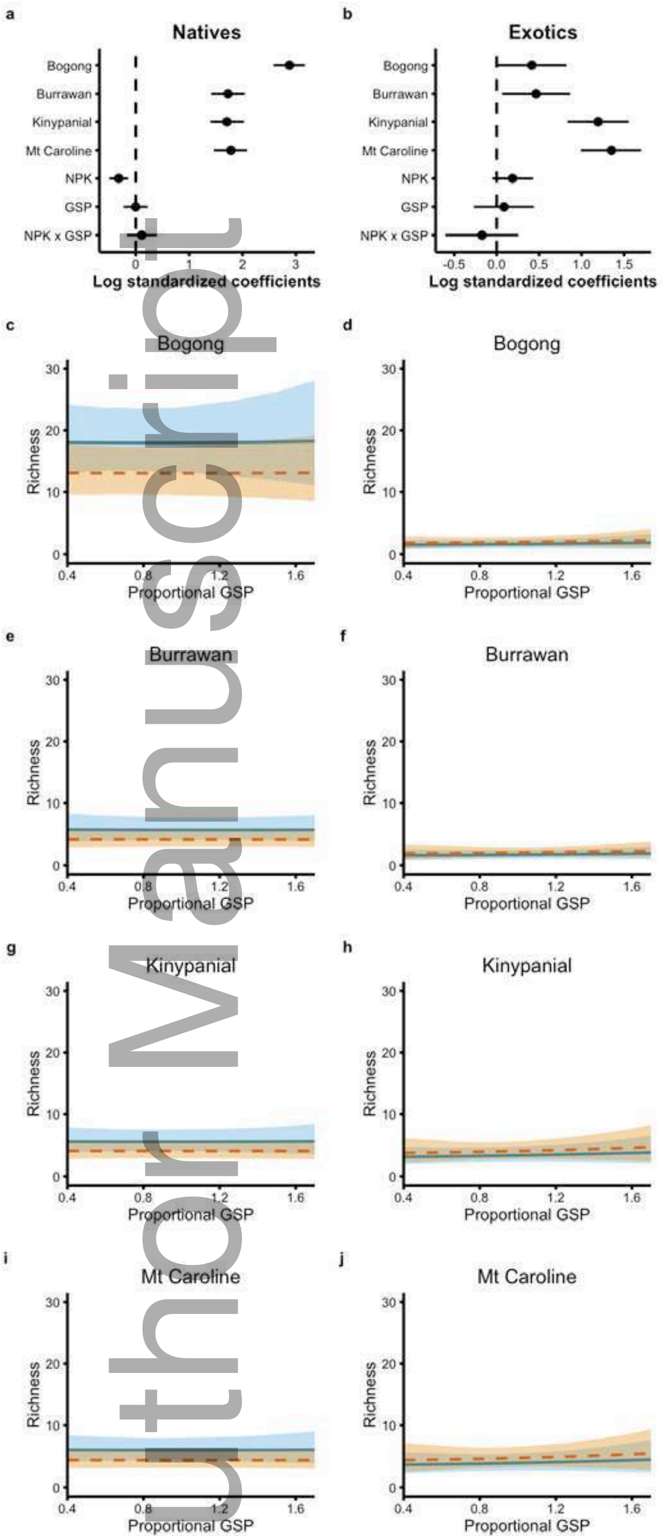

Fig. 6 Regression coefficients ± 95 Bayesian Credible Intervals for site random effects and each fixed effect in the model predicting a) native and b) exotic species richness. The Y-axis shows the site intercepts (Bogong, Burrawan, Kinypanial and Mt Caroline) interpreted as the log mean species richness in control conditions at mean long-term growing season precipitation (GSP). NPK, GSP and NPK x GSP are the modelled effects of NPK addition, GSP and their associated interaction on species richness, respectively. Response curves illustrating how native (c,e,g,i) and exotic (d,f,h,j) species richness changes with both NPK treatment and GSP. Dashed orange lines = NPK conditions, solid blue lines = Control; 95% credible intervals shown**.**