

# Measuring competitive impact: joint-species modelling of invaded plant communities

**Running title:** Measuring competitive impact.

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**Keywords:** abundance, biotic interaction, grasslands, invasive species, impact, joint species distribution model, light competition, tobit regression.

**Type of article:**

Research article

**Manuscript contains:**

Abstract – 299 words

Main text – 4, 641 words

References – 54

Figures – 6

Appendices – 3

Supplementary figures – 4

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## Abstract

1. Non-native species can dominate plant communities by competitively displacing native species, or because environmental change creates conditions favourable to non-native species but unfavourable to native species. We need to disentangle these alternative mechanisms so that management can target competitively dominant species and reduce their impacts.

2. Joint-species distribution models (JSDMs) can potentially quantify competitive impacts by examining how species respond to environmental variation and to changes in community composition. We describe a JSDM to model variation in plant cover, which detected declines in species abundance in the presence of a dominant competitor.

3. We applied our model to an experiment in an invaded grassy-woodland community in Australia where we manipulated biomass removal (through slashing and grazing by kangaroos) along a fertility gradient. Non-native species dominated plant cover at high fertility sites in the absence of biomass removal. Using a JSDM, we determined that three of the 72 non-native plant species (*Bromus diandrus*, *Acetosella vulgaris* and especially *Avena fatua*) were having a strong competitive impact on the community, driving changes in composition and reducing the cover of both native and non-native species, particularly in the absence of grazing. The dominant annual grasses (*Bromus diandrus* and *Avena fatua*) were two of the tallest species in the community and were good competitors for light under conditions of high fertility and low grazing. Consequently, their impacts were greatest on smaller statured species.

4. Synthesis. We demonstrate a method to measure competitive impact using a JSDM, identify species driving compositional change through competitive displacement, and identify where on the landscape competitive impacts are greatest. This information is central to managing plant invasions: by targeting dominant non-native species with large competitive impacts, management can reduce impacts where they are greatest. We provide details of the modelling procedure and reproducible code to encourage further application.

## Introduction

Dominance by non-native plant species is frequently associated with declines in the abundance and diversity of native species (Vilà et al., 2011). These changes can occur if non-native species are superior competitors, such that increasing abundance of non-natives directly drives declines in native species through competitive displacement (Levine et al., 2003; MacDougall, Gilbert, & Levine, 2009). Alternatively, increasing dominance by non-native species could be a consequence of changing environmental conditions that favour non-natives over natives due to species in each group having different environmental tolerances (HilleRisLambers, Yelenik, Colman, & Levine, 2010; Shea & Chesson, 2002). As plant invasions are frequently accompanied by environmental perturbations (Pysek et al., 2010; Vellend et al., 2017), it can be difficult to determine when non-native dominance is driven by competitive impact (Godsoe, Franklin, & Blanchet, 2017; Soberón, 2010). In fact, many non-native species appear to have little impact on the communities they invade (Lai, Mayfield, Gay-des-combes, Spiegelberger, & Dwyer, 2015; Williamson & Fitter, 1996). In order to manage non-native species appropriately, we need ways to identify which non-native species, if any, are having strong competitive impacts, and where those impacts are greatest (Gallien, Münkemüller, Albert, Boulangeat, & Thuiller, 2010; Ricciardi, Hoopes, Marchetti, & Lockwood, 2013).

Species distribution models have the potential to account for competitive impacts and species responses to environmental conditions by using community composition data from sites along known environmental gradients (Kissling et al., 2012; Nieto-Lugilde, Maguire, Blois, Williams, & Fitzpatrick, 2018). Joint-species distribution models (JSDM) simultaneously estimate the environmental responses of multiple species, and partition residual variation between co-occurring species (covariation). Many authors interpret covariation as representing species interactions such as competition (Latimer, Banerjee, Sang, Mosher, & Silander, 2009; Ovaskainen, Hottola, & Shtonen, 2010; Pollock et al., 2014; Warton et al., 2015). Large negative residual covariance can be observed where one species competitively displaces a second from

53 sites that both species could occupy. However, non-native dominance can have more nuanced  
54 impacts than just complete exclusion (Seabloom et al., 2013), requiring greater resolution that  
55 co-occurrence data can provide. Here we use a method proposed by Clark et al. (2017) that  
56 overcomes the problem of zero-inflation that is inherent in abundance data (see: *Joint-species*  
57 *tobit modelling in Methods*; Fig. 1). With this approach, we can detect declines in species  
58 abundance due to competitive displacement, in addition to complete exclusion.

59  
60 Even with these advances, separating environmental responses from competitive impacts is  
61 challenging (Adler et al., 2018), suggesting we should apply JSDMs to systems where the  
62 primary environmental drivers of species abundances are well understood (Giannini, Chapman,  
63 Saraiva, Alves-dos-Santos, & Biesmeijer, 2013; Wisz et al., 2013; Zurell, Pollock, & Thuiller,  
64 2018). In grasslands around the world, non-native plant species often increase in dominance at  
65 higher fertility sites and when grazing is excluded (Seabloom et al., 2015). This shift in  
66 dominance is attributed to competitive displacement of native species by non-native species.  
67 Species compete intensely when belowground resources are abundant (high nutrient and water  
68 availability; Harpole et al., 2016; Harpole & Tilman, 2006), leading to reductions in community  
69 diversity and dominance by competitively superior species. Where competition is intense,  
70 competitive superiority is expected to be related to differences in species traits (Kraft, Godoy, &  
71 Levine, 2015). Many non-native grassland species have traits associated with rapid growth and  
72 high biomass (Ordonez & Olff, 2013; Van Kleunen, Weber, & Fischer, 2010), traits that are likely  
73 beneficial when there is little above ground disturbance and competition for light is intense  
74 (Borer et al., 2014; Hautier, Niklaus, & Hector, 2009). These differences would be less important  
75 under herbivory (Lind, Borer, & Seabloom, 2013), reducing the competitive impact of dominant  
76 species.

77  
78 We aim to test these ideas using data from a 7-year experiment that tracked changes in plant  
79 cover over time following herbivore exclusion (Driscoll, 2017). Sites were arrayed along a

fertility gradient which allowed us to test whether the relationship between non-native dominance and resource availability is driven competitive impact. We used a JSDM to model how species cover varied with fertility, grazing and rainfall, and identified species with strong negative residual covariances, suggestive of strong competitive impacts on the community. We predicted that: 1) competitive impacts, and hence the magnitude of negative residual covariances, would increase in the absence of grazing where competition for light would be most intense; and 2) if competition for light caused competitive displacement, the strength of negative covariances between species (reflecting the strength of competitive interactions) should correlate with trait differences associated with growth and light capture.

## Methods

### Study system

This study was carried out in a box-gum grassy woodland reserve in south-eastern Australia (Pinnacle Reserve, ACT. 35° 15' S, 149° 02' E; 620 - 708 m a.s.l.). The vegetation of the reserve comprised a scattered overstorey of trees, predominantly *Eucalyptus blakelyi* and *E. melliodora*, with a dense understorey of grasses and forbs. The vegetation has been extensively modified over the last 150 years, primarily by tree clearance and livestock grazing. Livestock grazing ceased in the reserve in 1993 and the dominant herbivore is now the native eastern grey kangaroo (*Macropus giganteus*), which was at moderately high density over the course of the study (1.8 – 2.2 ha<sup>-1</sup>; Driscoll 2017). The understorey vegetation was dominated by a mix of native and non-native species, with many non-native species introduced for pasture improvement (e.g. *Dactylis glomerata* and *Trifolium subterraneum*) or as pasture contaminants (e.g. *Avena fatua* and *Bromus diandrus*). Mean annual precipitation in the area was ~660 mm year<sup>-1</sup> and daily maximum temperatures range from 9 °C to 33 °C during the spring growing period and as low as 4 °C in the preceding winter months (Australian Government Bureau of Meteorology, 2017). Soils are typically low fertility, shallow and rocky, although some deeper soils occur on slopes and in depressions.

107

108 Data collection

109 We used data from an experiment that tested whether different management interventions  
110 can increase native grassland species richness (Driscoll, 2017). In 2010, ten sites were  
111 established along a fertility gradient (see below). Sites ranged from relatively uninvaded  
112 communities to communities dominated by non-native species. Each site contained 10  
113 permanently marked 5 m x 5 m plots separated by at least 1 m. One of 10 different experimental  
114 treatment was applied to each plot, but we use only a subset of the treatments in this study (see  
115 Appendix 1, Fig S1). From 2011, five plots at each site were fenced in a single enclosure to  
116 exclude mammalian herbivores (predominantly kangaroos but also rabbits). One plot inside and  
117 one plot outside the fence had its above-ground biomass removed each year by slashing, and  
118 one plot inside and one plot outside the fence was left unmanipulated (unslashed). We analysed  
119 these four treatments at each site (grazed, unslashed; grazed, slashed; fenced, unslashed; and  
120 fenced, slashed), allowing us to test whether the competitive impact of non-native species was  
121 stronger in the absence of biomass removal by grazing and/or slashing, and to assess whether  
122 biomass removal by slashing had similar effects to herbivore grazing.

123

124 Vegetation surveys were conducted every year from 2010 to 2016, except for 2014. In late  
125 spring (October) of each year, the percent cover of all vascular plant species was visually  
126 estimated in four 1 m x 1 m quadrats placed in the corners of each plot (only three quadrats per  
127 plot were surveyed in 2013 due to time constraints). We use plant cover as a proxy of  
128 abundance because abundance scales can vary significantly between species. Our dataset thus  
129 comprised six years of vegetation cover data from 160 quadrats across 40 plots. In total, we had  
130 920 quadrat level vegetation measurements, comprising 10,780 cover estimates for 142 species  
131 (70 native and 72 non-natives; see Appendix 1, Fig. S2 for more details). In 2015 and 2016, we  
132 measured the traits of abundant species, defined as those comprising the first 80% of total  
133 recorded cover at each site. At each site, we measured traits associated with growth rate and

light capture on 5-10 adult individuals in each of the unslashed plots following standard protocols (Pérez-Harguindeguy et al., 2013) including canopy height (m), maximum height (m), canopy width (m), leaf length and width (cm) and specific leaf area ( $\text{mm}^2 \text{mg}^{-1}$ ; SLA). To avoid the influence of outliers, we used 90<sup>th</sup> quantile values from all measured plants to estimate species maximum potential for each trait.

Total extractable nitrogen at sites along the fertility gradient ranged from 615 ppm to 2420 ppm (Driscoll & Strong, 2017). Total soil carbon, nitrogen and phosphorus levels, as well as extractable nitrogen and phosphorus, all covaried strongly across the 10 sites (Appendix 1), and we used total extractable nitrogen as a proxy for overall soil fertility. Grasslands in this region also respond strongly to variation in annual rainfall (Prober, Thiele, & Speijers, 2013; Fig. S3). We obtained data on total rainfall in the four months prior to each survey (August – November) from the Australian Bureau of Meteorology (BOM, Appendix 1) as a proxy for water availability. Total rainfall during these months ranged from 185 – 414 mm over the seven years of the study. Both total nitrogen and spring rainfall were centred and scaled prior to model fitting.

## Analyses

### 1) *Relative dominance of non-native species.*

We examined how the dominance of non-native species changed over time, in relation to soil fertility, and in response to the experimental treatments (fencing and slashing). Our response variable was the proportion of non-native species cover in each plot in each year. This was calculated by taking the average cover of each species across quadrats in each plot in each year, summing these averages to get the total average cover of all species in each plot in each year, and calculating the proportion of total cover comprising non-native species. We logit-transformed this proportion and modelled it as a linear function of soil fertility, fitting a separate intercept and slope for each experimental treatment (grazed/fenced and slashed/unslashed) and for each year. We included rainfall as an additional explanatory

variable, specifying a single coefficient for the effect of inter-annual rainfall variation on the proportion of non-native cover. The model structure is described in detail in Appendix 2.

## 2) *Joint-species tobit modelling*

To test if dominance by non-native species was a consequence of environmental responses or competitive displacement, we specified a JSJM that modelled the cover of each species in response to variation in soil fertility, rainfall and experimental treatment (JSJM1). This model included a single covariance matrix to capture unexplained residual variation. We fitted a second model (JSJM2) to test whether competitive impacts were greater in fenced plots. JSJM2 had the same structure as JSJM1, but separate residual covariance matrices for each experimental treatment. We analysed data for the years 2013-2016, which were the years during which the experimental treatments showed clear effects (see: Figs 2 & S4b), and restricted our analyses to species present in >20% of plots measured between 2013 and 2016 (N = 30, 14 native and 16 non-native species; Fig S2.) These species were present at >50% of sites in each year and were thus sufficiently widespread that absences were more likely due to unsuitable environmental conditions or competitive displacement rather than dispersal limitation. We analysed cover data at the quadrat level because we expected species interactions to be most evident at this scale. Zero cover was recorded when a species was absent from a quadrat. Even after restricting our analysis to the 30 most common species, most of our data comprised zero values (~69%; 4,396 cover estimates, 10,004 absences).

We used tobit regression to accommodate zero inflation by treating absences as censored data (Clark et al., 2017; Tobin, 1958). Censored data occur when it is not possible to observe a value beyond some limit. In this case, we assume there is an unobserved latent variable that measures the 'suitability' of each quadrat for each species, where suitability encompasses all biotic and abiotic factors that might influence species cover. When a species is present in a quadrat we equate the latent suitability with cover, assuming that higher cover indicates higher suitability (Fig. 1). Quadrats where species are absent can be thought of as sufficiently low



suitability that a species cannot persist but quadrats with zero cover can still vary in their underlying suitability. We model observations of zero cover as censored data arising from this latent suitability distribution, which can take values less than zero:

$$y = \begin{cases} y^*, & \text{if } y^* > 0 \\ 0, & \text{if } y^* \leq 0 \end{cases}$$

where  $y$  is the observed cover and  $y^*$  is the corresponding latent suitability value. To complete the model, we need to specify a distribution for the underlying latent variable. We specified the underlying distribution as multivariate normal with 30 dimensions, one for each species.

We regressed latent suitability ( $y^*$ ) against the environmental variables soil fertility and rainfall, with residual variation captured in a single covariance matrix (JSDM1). We specified different regression coefficients for each experimental treatment, modelled hierarchically, and included normally distributed random effects to account for repeated measurements of plots nested within sites. The structure of JSDM1 was:

JSDM 1:

$$\mathbf{y}_{[ijkl]}^* \sim \text{MultiNormal}(\boldsymbol{\mu}_{[ijkl]}, \boldsymbol{\Sigma})$$

$$\boldsymbol{\mu}_{[ijkl]} = \begin{pmatrix} \mu_{1[ijkl]} \\ \mu_{2[ijkl]} \\ \vdots \\ \mu_{N[ijkl]} \end{pmatrix}$$

$$\mu_{s[ijkl]} = \beta_{\text{intercept}_{S[j]}} + \beta_{\text{slope}_{S[j]}} \cdot \text{fertility}_{[jk]} + \beta_{\text{rain}_{S[j]}} \cdot \text{rainfall}_{[i]} + \beta_{\text{plot}_{[jk]}}$$

$$\beta_{\text{plot}_{[jk]}} \sim \text{Normal}(\beta_{\text{site}_{[k]}}, \sigma_{\text{plot}}^2)$$

$$\beta_{\text{site}_{[k]}} \sim \text{Normal}(0, \sigma_{\text{site}}^2)$$

where  $\mathbf{y}_{[ijkl]}^*$  is an  $N$ -length vector of latent suitability values in year  $i$  (1-3), under treatment  $j$  (1-4), at site  $k$  (1-10) in quadrat  $l$  (1-4).  $s$  indexes species ( $s = 1 \dots N$ ) with intercept terms measuring average site suitability for each species in each treatment, and slope and rain terms measuring how site suitability varied with soil fertility and rainfall for each species in each treatment.  $\Sigma$  is an  $N \times N$  covariance matrix with the diagonal containing the residual variances in suitability for each species,  $\sigma^2$ , and the off-diagonals containing the residual covariances between each species pair, conditional on the value of  $\mu_{[ijkl]}$ . This matrix has  $N * (N - 1) / 2 = 435$  unique elements, with the covariance between two species defined as:  $\Sigma_{12} = \sigma_1 \sigma_2 \rho_{12} = \Sigma_{21}$ .

The covariances describe how residual variation in the cover of one species is related to residual variation in the cover of a second species. If, having accounted for environmental effects, the cover of one species declined in quadrats when the cover of a second species increased, the residuals of the two species would covary negatively. We interpreted negative covariances as due to competition on the grounds that we had modelled species responses to the major environmental gradients in these grasslands (fertility and water availability) (Leishman & Thomson, 2005; Morgan et al., 2016; Prober, Thiele, & Speijers, 2016). Large negative covariances imply potentially strong competitive impacts, while species with low cover, or where cover is well explained by environment variables, will have smaller covariances because there is less residual variation that could be associated with co-occurring species. Moreover, if a dominant species causes several species to decline in cover, resulting in strong negative covariances, this is likely to induce a pattern of positive covariances among the impacted species because they would all tend to have lower cover at sites where the dominant species was present and higher cover at sites where it was absent.

### 3) *Change in species covariances by treatment*

Specifying a single covariance matrix in JSMD1 meant the covariances were estimated from the data in all treatments. In JSMD2, we specified a separate covariance matrix for each of the four treatments:

JSMD2:

$$\mathbf{y}_{[ijkl]}^* \sim \text{MultiNormal}(\boldsymbol{\mu}_{[ijkl]}, \boldsymbol{\Sigma}_{[j]})$$

$$\mu_{s[ijkl]} = \beta_{\text{intercept}_{s[j]}} + \beta_{\text{slope}_{s[j]}} \cdot \text{fertility}_{[jk]} + \beta_{\text{rain}_{s[j]}} \cdot \text{rainfall}_{[i]} + \beta_{\text{quadrat}_{[jkl]}}$$

where both the coefficients for species  $s$  and the covariances  $\boldsymbol{\Sigma}$  varied with treatment  $j$  (1-4).

Comparing the covariance matrices for different treatments in JSMD2 allowed us to evaluate whether competitive interactions were stronger in plots where herbivores were excluded.

#### 4) *Predicting competitive impact from functional traits*

We predicted that competitive impacts, measured as the magnitude of negative covariance between species, should be linked to differences in traits associated with growth and light capture. To test this, we regressed the posterior mean of the negative covariance parameters estimated in JSMD2 against the absolute difference in measured trait values for each species pair. Trait values were normalised prior to analysis so that traits measured using different units could be compared directly. For the regression models, we specified separate intercept and slope coefficients for the covariance-trait relationships in each experimental treatment, with the slopes and intercepts modelled as drawn from normal distributions for each trait.

All models were fitted to the data in a Bayesian framework using adaptive Hamiltonian Monte Carlo with the probabilistic programming language Stan (Carpenter et al., 2017) and the rstan interface (Guo et al., 2016) in R, version 3.4 (R Core Team, 2016). Details of model fitting and prior specification are in Appendix 2 and online at <https://github.com/aornugent/impact2>. We took a conservative approach to identifying interactions in the data by specifying that we  $a$

*priori* expected covariances to be weak (see prior specification in Appendix 2), meaning that strong residual covariances required strong support from the data.

## Results

### 1) *Relative dominance of non-native species*

Overall, the proportion of total cover that comprised non-native species increased with increasing soil fertility (Figs 2, S4a). Prior to and immediately after fencing (2010 & 2011), the relationship between fertility and proportion of non-native cover was similar in the fenced and grazed plots, and in the slashed and unslashed treatments. However, from 2012 onwards the proportion of non-native cover increased substantially at higher fertility sites in the fenced, unslashed plots (i.e., in the absence of biomass removal). There was no clear change over time in the proportion of non-native cover along the fertility gradient in plots that were grazed, slashed or both (Figs 2, S4b). The proportion of non-native cover was higher in years with higher spring rainfall (Fig. S3a)

### 2) *Joint species tobit modelling*

Species responded differently to changes in soil fertility, with latent site suitability increasing strongly with higher soil fertility for two native and five non-native species (95% credible intervals above zero in at least one treatment; Fig. 3). The remaining species, both native and non-native, declined in cover with increasing fertility. Relationships between cover and fertility did not vary much between experimental treatments with three exceptions: relative to other species, the cover of the non-native species *Avena fatua*, *Bromus diandrus* and *Acetosella vulgaris* increased more strongly with fertility in the fenced, unslashed treatment. At high fertility, several fenced, unslashed plots were completely dominated by one or more these species. For most species, cover was positively related to rainfall across years (Fig. S3b).

Figure 4 shows species' residual covariances from JSMD1 as a pairwise covariance matrix (Fig. 4b) along with the median covariance for each species across all pairwise interactions (Fig. 4a). We report the median covariance because covariance values could be highly skewed. One species, *Avena fatua*, stood out as having strong negative covariances, with high cover of *A. fatua* often associated with reduced cover of other species. Median covariance for the native grass *Themeda triandra* was the second most negative but of much smaller magnitude than *A. fatua*. Moreover, *T. triandra* covaried negatively with *A. fatua* (Fig. 4b), such that high cover of *A. fatua* was associated with low cover *T. triandra* and vice versa. Small-statured species, such as in the genera *Aira*, *Vulpia* and *Hypochaeris*, tended to covary positively.

### 3) Change in species covariances by treatment

JSMD2 revealed that species' residual covariances varied by grazing and slashing treatment (Fig. 5), suggesting that competitive interactions were altered by biomass removal. Covariances were weakest in the grazed, slashed treatment with the median close to zero for most species (mean median covariance with 95% confidence intervals = -0.4, CI -2.2 to 1.3), implying weak interactions. Covariances were larger but still relatively weak in the fenced, slashed treatment (mean = 0.2, CI -1.5 to 2). Median covariances were most negative in the grazed, unslashed treatment (mean = -1.3, CI -3 to 0.5) and especially the fenced, unslashed treatment (mean = -3.2, CI = -4.9 to -1.5), suggesting stronger competitive interactions in the absence of slashing, and especially in the absence of both grazing and slashing. Relative to the natural situation in these grasslands (the grazed, unslashed treatment), the three species whose cover increased most strongly with fertility in the fenced, unslashed plots (*Avena fatua*, *Bromus diandrus* and *Acetosella vulgaris*) showed a marked shift to more negative covariances in the same treatment, especially *A. fatua* (Fig. 5). This implies these species had a greater competitive impact on other species in the absence of biomass removal.

### 4) Predicting impact from functional traits

In the fenced, unslashed treatment, stronger negative covariances between species were associated with greater differences in plant height (Fig. 6). This relationship was evident, though weaker, in the grazed, unslashed treatment but largely absent in both slashed treatments. Negative covariance decreased between species that had greater differences in SLA, but this relationship did not explain positive covariances between species. None of the remaining trait differences (canopy width and leaf dimensions) showed strong relationships with covariances.

## Discussion

Measuring the strength of species interactions when these are confounded with environmental variation remains a major obstacle to studying the impact of non-native species in plant communities (HilleRisLambers et al., 2010; Levine et al., 2003; MacDougall & Turkington, 2005). We have shown how a joint-species-distribution model can be adapted to model plant cover and, when applied to our case study, could identify the non-native species having large competitive impacts on the community, as well as where those impacts were greatest. Globally, non-native species frequently dominate grasslands under conditions of high fertility in the absence of grazing (Seabloom et al., 2013, 2015). Our findings show this can result from displacement of native species by one or more competitively dominant non-native species. In our study, greater cover of three non-native species (*Bromus diandrus*, *Acetosella vulgaris* and especially the annual grass *Avena fatua*) was associated with strong declines in the cover even after accounting differences in environmental responses. This outcome is consistent with previous studies on the impact of non-native species in Australian temperate grasslands (Driscoll, 2017; Driscoll & Strong, 2017; Prober, Thiele, Lunt, & Koen, 2005) and matching outcomes in grasslands globally (Chang & Smith, 2014; Flores-Moreno et al., 2016; Harpole et al., 2016).

Our results support the predictions outlined in the Introduction. First, competitive impacts, as revealed by the strength of negative covariances, were much stronger in the absence of biomass removal (Fig. 4). Second, under low or no biomass removal, the strength of negative covariances were linked to differences in plant height: in unslashed plots, taller species had greater impact on shorter species, implying a strong competitive advantage associated with plant height under these conditions (Fig. 6). This outcome most likely results from competition for light, which should favour taller, higher biomass species (Borer et al., 2014; Hautier et al., 2009). While negative covariances were linked most strongly to height differences, negative covariances were smaller among species with greater differences in specific leaf area (Fig. 6). This implies that, while competitive dominance was due primarily to a trait advantage in height, this was partly offset by trait dissimilarity in SLA, potentially indicative of reduced competitive impact through niche differentiation (Gross, Börger, Duncan, & Hulme, 2013).

Results from the JSDMs provide additional insights into interactions in these grasslands. For example, negative covariances, and hence competitive interactions, were weaker in the slashing treatments (Fig. 5). Annual biomass removal by slashing may prevent species from attaining cover sufficient to have a strong competitive impact (Mortensen et al., 2018). Grazing may also prevent competitive dominance, although interactions were stronger under grazing alone than when plots were slashed (Fig. 5), suggesting grazing removes less biomass than slashing, or selectively removes certain species allowing others to attain cover sufficient to have measurable impact (Evju, Austrheim, Halvorsen, & Mysterud, 2009). The most dominant species, *Avena fatua* had the greatest competitive impact, but also covaried negatively with two other species that had relatively high impact overall: the native grass *Themeda triandra* and non-native forb *Acetosella vulgaris* (Fig. 4). *Avena fatua* and *A. vulgaris* both increased in cover at higher fertility in the absence of biomass removal, suggesting these species competed for site occupancy under those conditions. The ability of *A. vulgaris* to form dense rhizomatous mats may have excluded *A. fatua* from some sites (Fan & Harris, 1996). *Themeda triandra*, in contrast, had higher cover at

lower fertility. *Themeda triandra* is known to dominate more intact native grasslands (Prober & Lunt, 2009), suggesting that *A. fatua* may be displacing an otherwise competitively dominant native grass at higher fertility sites.

Other non-native species were abundant in these grasslands but had little or no competitive impact. Short-statured annual grasses in the genera *Aira* and *Vulpia*, for example, were widespread (Fig. S2) and had high average cover where they occurred (15% and 24% for *Aira* and *Vulpia*, respectively, compared with 30% for *Avena fatua*). Both *Aira* and *Vulpia* strongly negatively covaried with *A. fatua* and *B. diandrus*, and both covaried positively with other, typically short-statured, species that were also impacted by the competitive dominants. Hence, in addition to identifying the drivers of change in this community, we can identify non-native species that achieve moderate to large cover without impacting the community, most likely because they are ruderal-like species that exploit more marginal habitats.

We have demonstrated how a JSDM can be applied to field data to measure impact and identify the species driving compositional change in a plant community. We emphasise that interpreting negative residual covariation as due to species interactions relies on having measured and correctly modelled the major environmental variables controlling species abundances (Hui, Taskinen, Pledger, Foster, & Warton, 2015). Our approach of crossing a natural fertility gradient with manipulation of biomass removal no doubt helped to disentangle competitive from environmental effects in this system, as it meant differences between the biomass treatments at each site were not confounded with other environmental variables. Nevertheless, the model appeared successful in identifying species having impact in the unmanipulated treatment alone (grazed, unslashed; Fig. 5), suggesting JSDMs can detect interactions in systems without experimental manipulation where the environmental drivers are well understood.



There are additional choices to be made in applying JSDMs to field data. We limited our analysis to common species, in part because large covariance matrices are difficult to estimate due to the large number of parameters and associated computational costs, and because fewer data are available to estimate parameters for less common species. Recent modelling developments have attempted to overcome these issues by using latent axes to group species showing similar responses to unmeasured sources of variation (Hui et al., 2015; Taylor-Rodríguez, Kaufeld, Schliep, Clark, & Gelfand, 2017; Thorson et al., 2015). We chose not to do this because latent axes might capture the common response of species to one or more of the competitive dominants, meaning this signal of competition would be missing from the residual covariation. There was evidence for a common response in our results where short-statured species, such as in the genera *Aira* and *Vulpia*, tended to covary positively, most likely because these species all had low cover where the competitive dominants were abundant and increased in cover only where the competitive dominants were rare. Fitting the full residual covariance matrix allowed for the pattern of positive covariances that we would expect due to the competitive impact of one or more dominant species. Restricting our analysis to common species may also have downplayed the impact of competitive dominants because, for some species, rarity could be due to competitive displacement.

## Conclusion

Separating plant species responses to environmental variation from the outcome of species interactions is challenging (Adler et al., 2018). We have shown it is possible to quantify competitive interactions using a JSDM when we can measure or manipulate the major axes of environmental variation. This allowed us to identify the species driving compositional change through competitive displacement in a temperate grassland, to identify where on the landscape competitive impacts were greatest, and to identify widespread, abundant non-native species that had little or no impact on the community and thus were likely passengers of environmental change. We provide the data and code needed to reproduce our analyses in an R package

(<https://github.com/aornugent/impact2>) to encourage further application and model development.

## **Acknowledgements**

We thank ACT Territory and Municipal Services' Parks, the Friends of the Pinnacle community group and the many volunteers that have contributed to the ongoing collection of this dataset. The project was funded by an ACT Government Environment grant, the Australian Government's Caring for our Country program, and the Belconnen Labor Club. This work was supported by an Australian Research Council grant to RPD and JAC (DP150101839). We thank the reviewers whose comments helped improve the manuscript.

## **Author contributions**

AO, EW and RD conceived the study. DD designed and established the experiment. AO and DD collected data. AO developed the JSMD models. AO, EW and RD analysed data and model output. AO wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

## **Data accessibility**

Data and code used in this manuscript are freely available at <https://github.com/aornugent/impact2>

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## Figures:

Figure 1. A simulated example of tobit regression. Black circles show observed cover for a species measured at points along an environmental gradient. Cover declines as environmental suitability decreases, eventually reaching a point where the environment is unsuitable for the species and cover is zero. Beyond that point, environmental suitability continues to decline but cover remains at zero. These zero values are censored in that zero cover provides partial information about the latent suitability (open circles): it tells us a site is unsuitable but, beyond that, does not measure how unsuitable. Tobit regression aims to estimate latent suitability (the open circles, which are uncensored) by fitting a regression line (red) to the cover data, treating the zero values as censored.

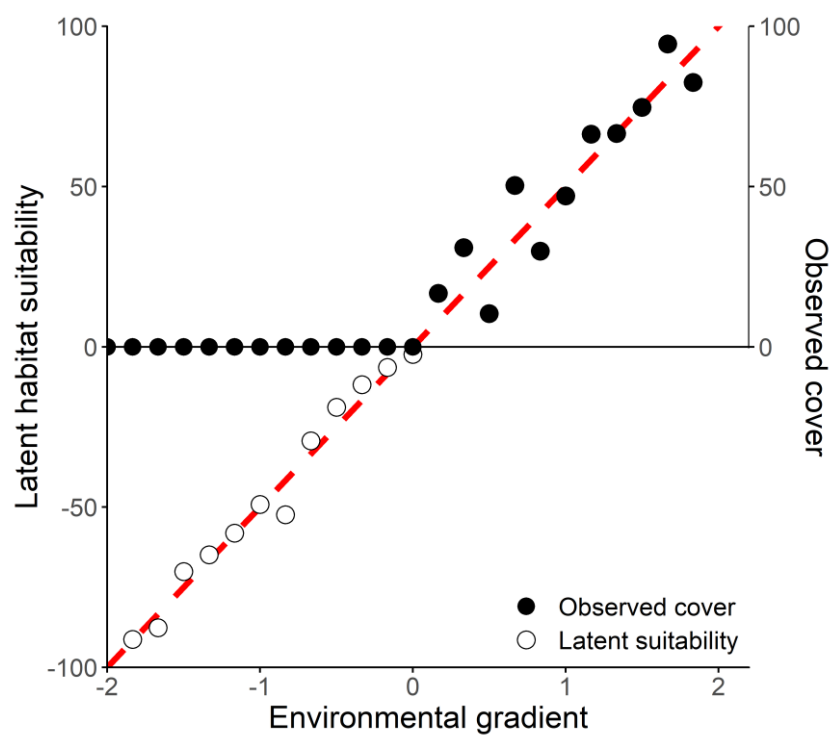
Figure 2. Proportional cover of non-native species (logit-transformed) as a function of soil fertility at 10 sites measured over 7 years (2010-2016 with no measurement in 2014). There were four treatments at each site, which are plotted separately. Slashed plots are shown on the top line and unslashed plots on the lower line, with filled circles and solid lines for fenced plots, and open circles and dashed lines for grazed plots. Fertility is scaled and standardized as described in Appendix 1.

Figure 3. Latent suitability with respect to soil fertility for 30 species estimated using a joint-species-distribution model and tobit regression (see text). Separate relationships were fitted for each species in each of four treatments, shown as different panels. Native species are drawn with dashed lines ( $n = 14$ ) and non-native species with solid lines ( $n = 16$ ). Lines are coloured from dark blue to light yellow corresponding to a shift from negative to positive slopes, respectively.

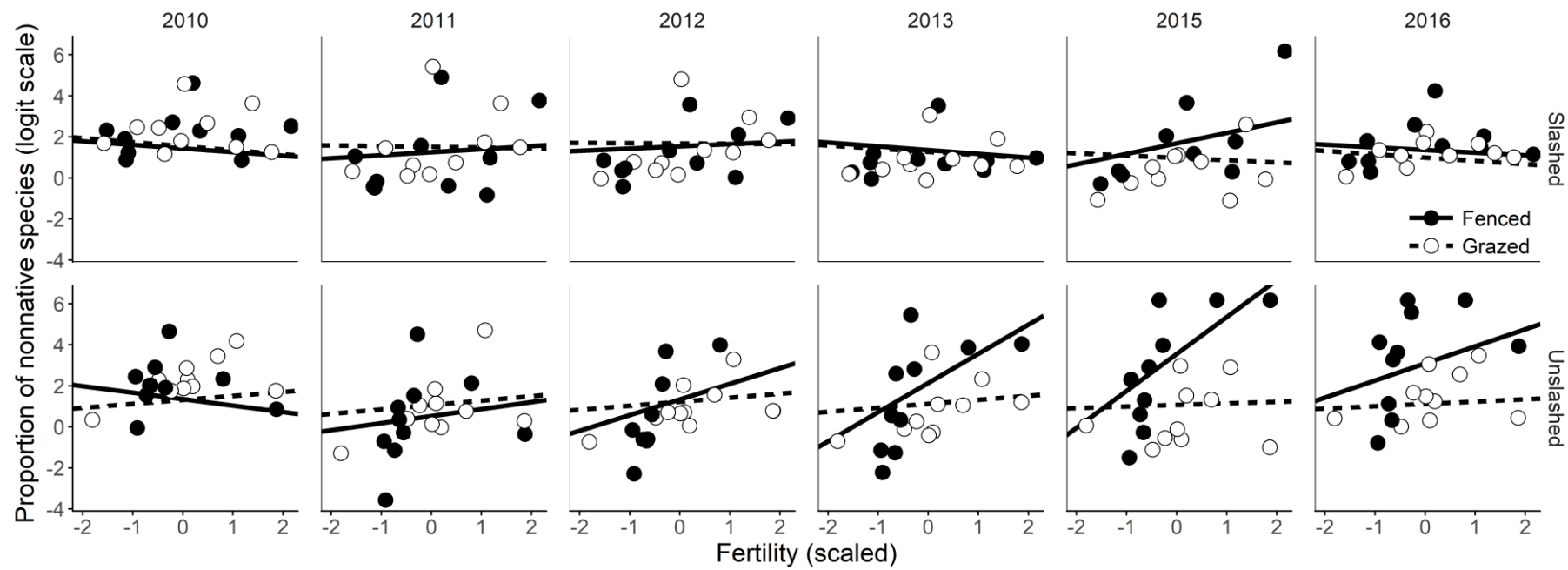
Figure 4. a) The median residual covariance from all pairwise interactions for each species and b) the full residual covariance matrix for JSMD1. Negative covariances are indicative of competitive displacement (see text). The full matrix shows mean covariances from the posterior distributions shaded by magnitude and direction, ranging from large negative covariances (deep red) to large positive covariances (blue). A black dot indicates the 95% credible intervals for a covariance did not include zero. Non-native species are marked with asterisks.

Figure 5. The median residual covariance from all pairwise interactions for each species from JSMD2, where a separate covariance matrix was fitted for each treatment (shown as separate panels). The median covariance summarises the magnitude of competitive displacement between a single species and the rest of the community. Names of non-native species are shown in black and native species in grey. Non-native species are marked with asterisks.

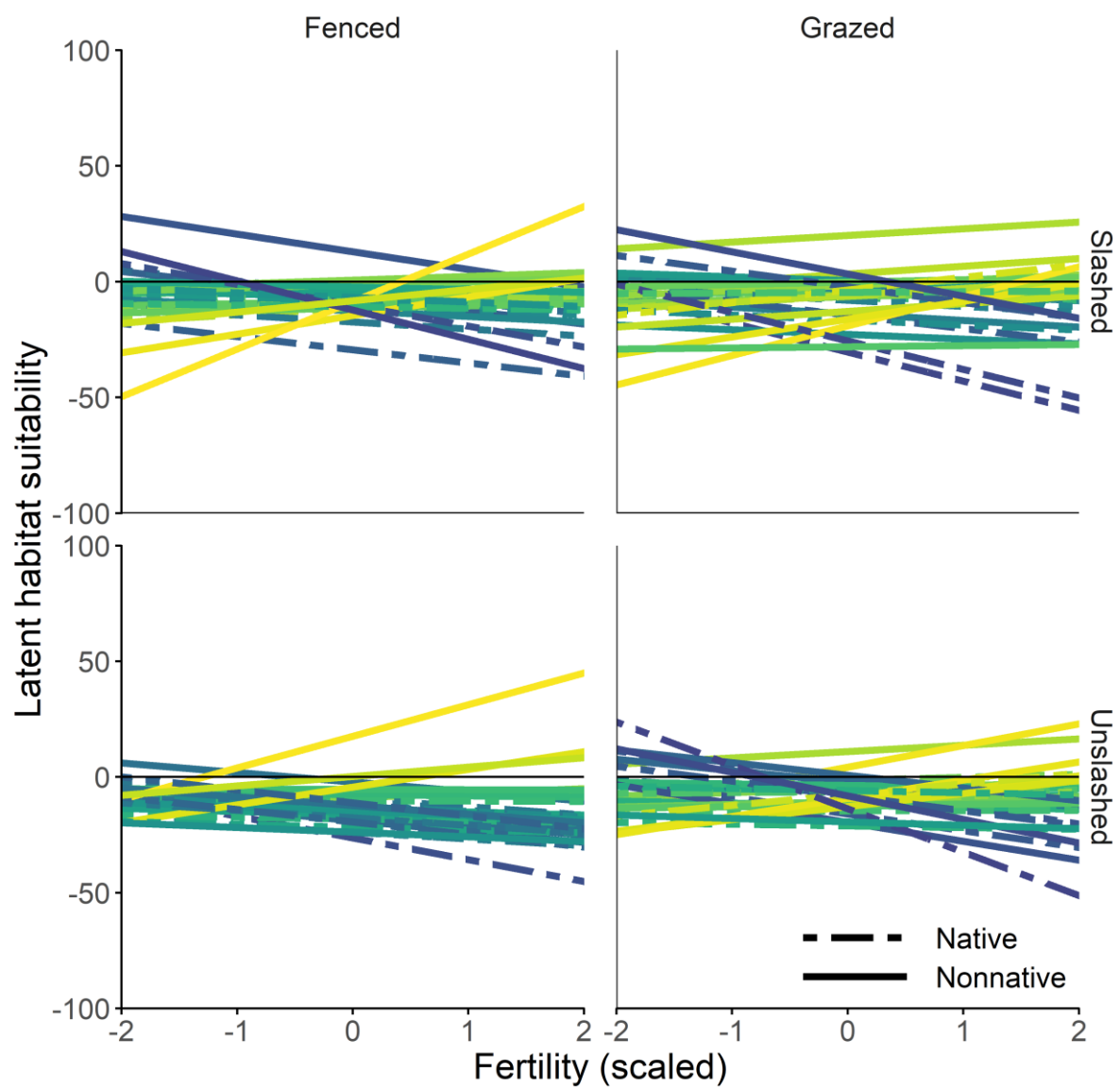
Figure 6. Mean (circles) and 95% credible intervals for the slope of the relationship between covariance and trait differences among species. Negative values indicate that competitive displacement is associated with a greater differences in trait values between species. The relationships are plotted separately for the four treatments, with filled circles for fenced plots, open circles for grazed plots, and slashed and unslashed plots in different panels. Trait differences were normalized before analysis to allow direct comparison of slope estimates for traits measured in different units.



**Figure 1.**

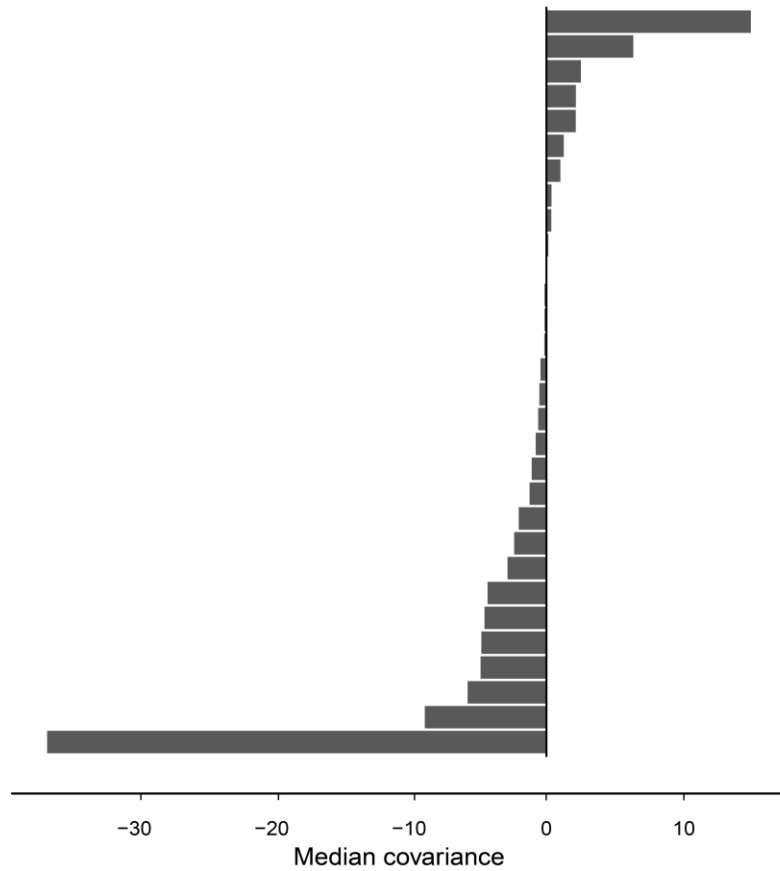


**Figure 2.**



**Figure 3.**

A



B

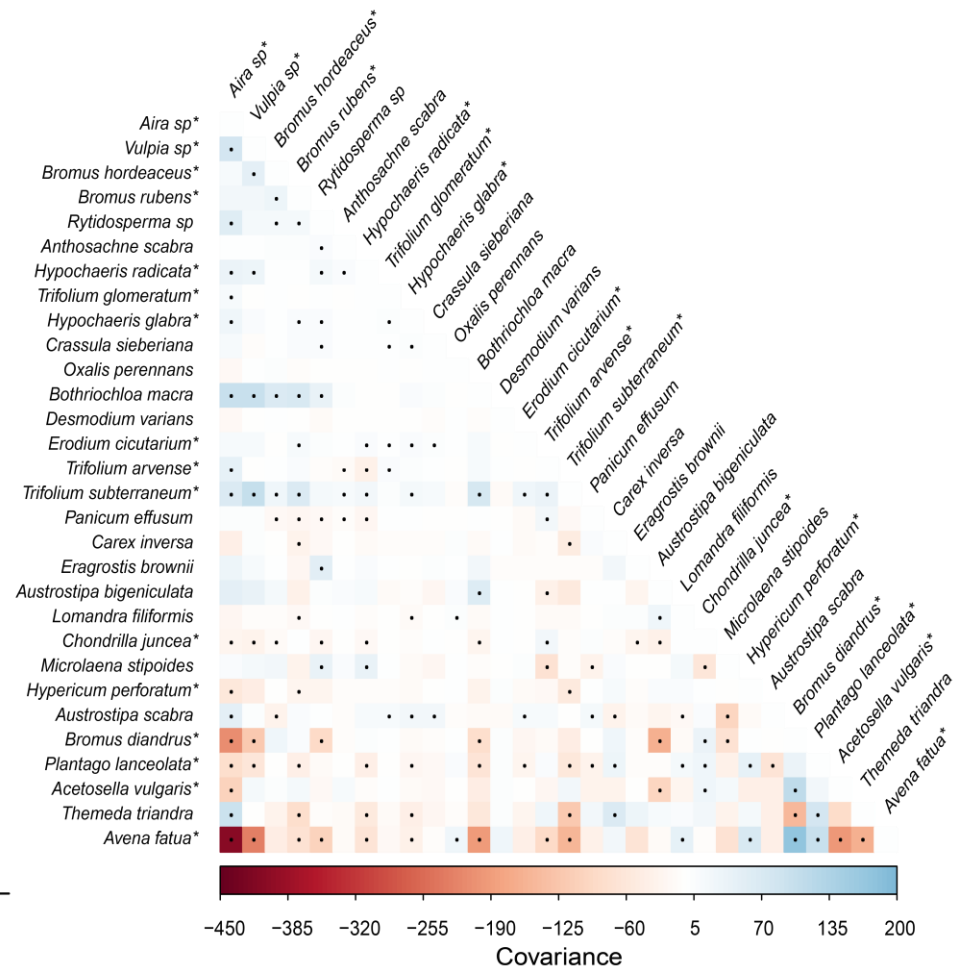


Figure 4.

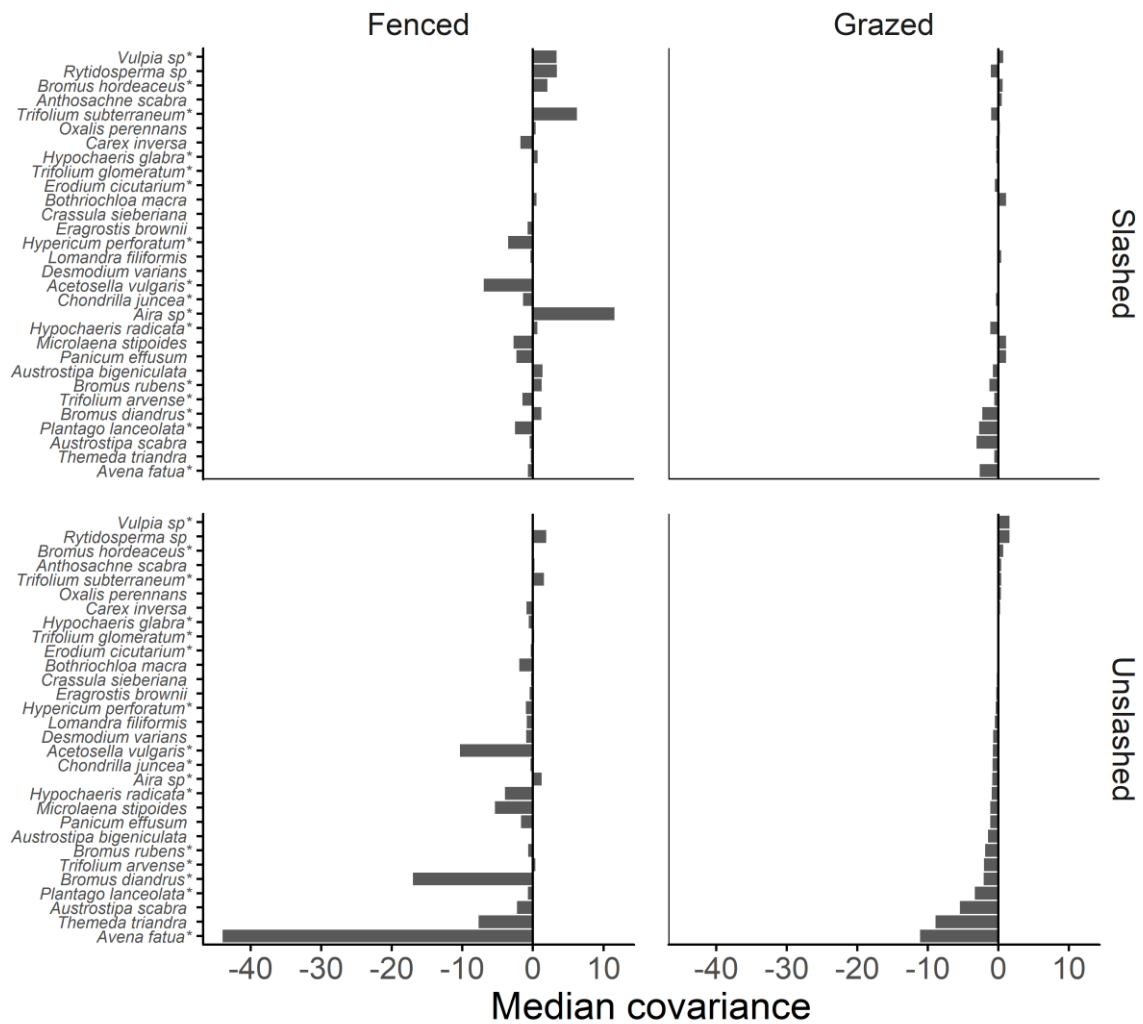
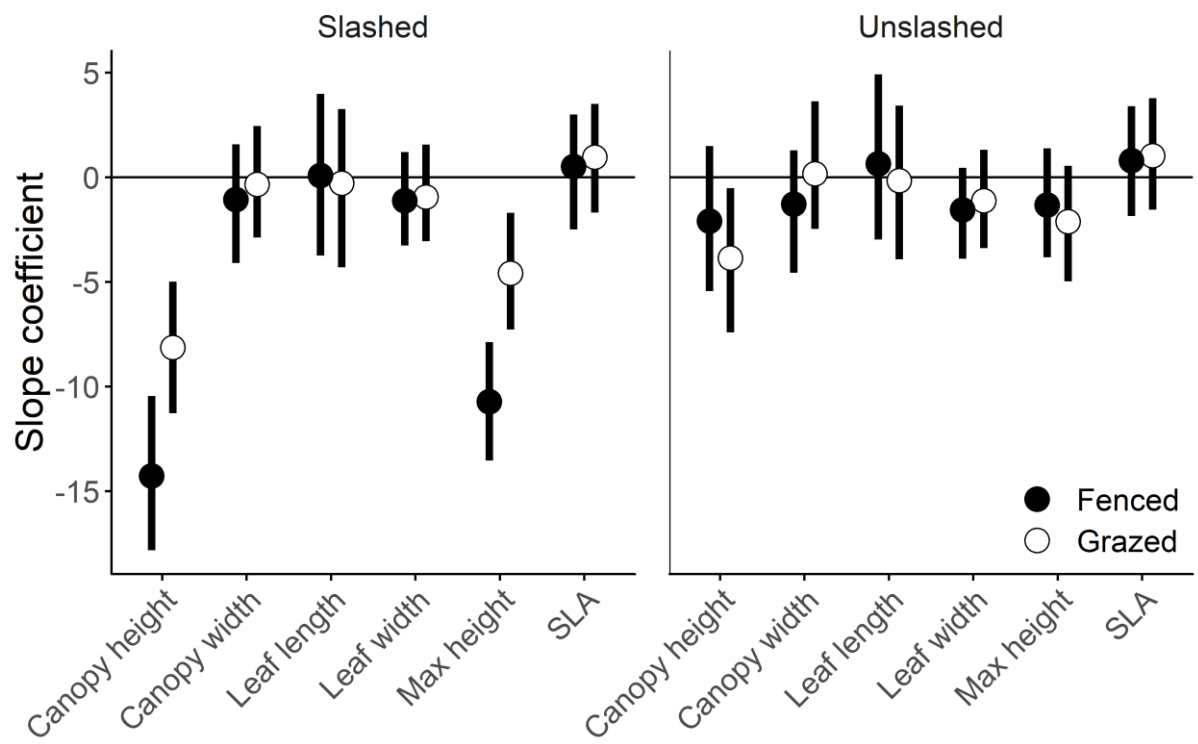


Figure 5.



**Figure 6.**